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Southeast Fisheries Center Miami Laboratory
National Marine Fisheries Service, NOAA
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CONFIDENCE LIMITS FOR POPULATION PROJECTIONS WHEN VITAL RATES VARY RANDOMLY

TIM GERRODETTE,[1] DANIEL GOODMAN,[2] AND JAY BARLOW[3]

ABSTRACT

Due to unpredictable future environmental changes, population growth is more realistically viewed as a stochastic than a deterministic process. Environmental variablity is modeled by allowing the population's survival and fecundity rates to be correlated random variables. The expected future population vector and its variance-covariance matrix are computed. The projected total future population size is approximately log-normally distributed, but confidence limits for future population size can be more accurately computed from the distribution of the realized factor of increase. Numerical examples illustrate how the calculation of confidence limits for future population size and of the probability that the population will increase in size can be applied to the management of living resources.

The predicted size of an age-structured population can be projected if its initial size, age distribution, and vital rates are known (e.g., Leslie 1945; Keyfitz 1968). Such population projections are commonly used in fisheries and wildlife management when age-specific fecundity and mortality rates are available. However, there is uncertainty in such projections. First, we rarely know vital rates exactly; rather, we have estimates of the true rates, and these estimates are subject to sampling and other types of errors. Second, the true rates themselves are not constant with time. Environmental conditions are always changing, and the vital rates would be expected to change in response. To an extent, the changes of conditions may themselves be forecast and incorporated into a population model. Some changes, however, are unpredictable, and these changes give rise to fluctuations in the vital rates which make our estimates of population size for some future time less certain. Nevertheless, it may still be possible to make probabilistic predictions about future population size given some statistical knowledge about the fluctuating vital rates.

In this paper we limit ourselves to consideration of the second of these problems, projecting age-structured populations when mortality and fecundity rates vary randomly with time. Recently this topic has been of interest and controversy in a more theoretical context (Boyce 1977; Cohen 1979a, b; Daley 1979; Tuljapurkar and Orzack 1980; Tuljapurkar 1982; Slade and Levenson 1982). In spite of earlier results to the contrary (Boyce 1977), analyses (Sykes 1969; Cohen 1977), and simulations (Slade and Levenson 1982) have shown that when vital rates fluctuate randomly with no serial correlation, the expectation of population size at a future time will be exactly equal to the population size projected using the mean vital rates in a deterministic projection. For application in fisheries and wildlife management, the problem is that the distribution of future population sizes will often be strongly skewed. This skew means that the mean and variance of future population size, even if known, are not sufficient to characterize the distribution and, in particular, not sufficient to compute confidence limits for total population size. In this paper we examine two transformations of this skewed distribution which approximate a normal distribution, and evaluate the accuracy of confidence limits computed from these transformations.

As pointed out by several of the authors cited above and earlier by Lewontin and Cohen (1969) for a non-age-structured population, stochastic effects can cause the modal or most likely population trajectory to decline to extinction, even though the expected or mean population size is growing at a geometric rate. Clearly, if we are to use population projections in fisheries and wildlife management, we should be concerned about the effects of natural variability on the results of our projections. In response to this concern, we have written two com-

[1]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[2]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Department of Biology, Montana State University, Bozeman, MT 59717.

[3]Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093; present address: Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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puter programs for stochastic population projections which can serve as research and management tools. Here we illustrate the utility of these programs with numerical examples, compare our results with recent theoretical analyses, and discuss the implications of these results to the management of living resources.

METHODS

Sykes (1969) presented three models for incorporating stochasticity into population projections. He concluded that the observed variability in human demographic projections was best described by his third model, in which the elements of the Leslie matrix (the effective fecundity rates and the survival rates) are random variables, each with a specified mean and variance, and with specified covariances between them. The model does not allow for serial covariance in vital rates between successive time periods.

Let $\boldsymbol{n}_t$ be a population vector of ω age classes at time t. The stochastic projection model is

$$\boldsymbol{n}_{t+1} = (\boldsymbol{A} + \boldsymbol{\Delta}_t)\,\boldsymbol{n}_t, \qquad t = 0, 1, 2, \ldots$$

where $\boldsymbol{A}$ is a constant projection matrix of mean vital rates and $\boldsymbol{\Delta}_t$ is a matrix of random deviations whose elements have a specified covariance structure $\{\mathrm{Cov}(\Delta_i,\Delta_j)\}$ but which are uncorrelated in time. Let $N_t = \sum_{i=1}^{\omega} n_{ti}$ be the total population size at time t. It is convenient to normalize the projected population to the initial population size and consider the distribution of the ratio N_t/N_0. The mean and variance of this ratio are given by

$$E(N_t/N_0) = E(N_t)/N_0 = \sum_{i=1}^{\omega} E(n_{ti})/N_0$$

and

$$\mathrm{Var}\,(N_t/N_0) = \mathrm{Var}\,(N_t)/N_0^2 = \sum_{i=1}^{\omega}\sum_{j=1}^{\omega} \mathrm{Cov}\,(n_{ti},n_{tj})/N_0^2.$$

From Sykes (1969, equations 19 and 20), the mean and variance of the population vector are given by

$$E(\boldsymbol{n}_t) = \{E(n_{ti})\} = \boldsymbol{A}^t \boldsymbol{n}_0$$

and

$$\mathrm{Var}\,(\boldsymbol{n}_t) = \{\mathrm{Cov}\,(n_{ti},n_{tj})\} = \sum_{k=0}^{t-1} \boldsymbol{A}^{t-1-k} \left\{ \sum_{\alpha=1}^{\omega}\sum_{\beta=1}^{\omega} \mathrm{Cov}\,(\Delta_{i\alpha},\Delta_{j\beta}) [\mathrm{Cov}\,(n_{k\alpha},n_{k\beta}) + E(n_{k\alpha})E(n_{k\beta})] \right\} \boldsymbol{A}'^{t-1-k}$$

where $\boldsymbol{A}'$ is the transpose of $\boldsymbol{A}$ and where the curly brackets indicate that the expression inside them is the ith element of the vector or the ijth element of the matrix considered.

Tuljapurkar and Orzack (1980) predict that for large t, N_t/N_0 will be lognormally distributed. The mean and variance of the normally distributed variable $\log\,(N_t/N_0)$ are calculated from the mean and variance of the lognormally distributed variable N_t/N_0 by

$$E[\log(N_t/N_0)] = \log[E(N_t/N_0)] - \left\{\frac{\mathrm{Var}[\log(N_t/N_0)]}{2}\right\}$$

and

$$\mathrm{Var}\,[\log\,(N_t/N_0)] = \log\left\{\frac{\mathrm{Var}\,(N_t/N_0)}{[E(N_t/N_0)]^2} + 1\right\}$$

(Aitchison and Brown 1957). We have found in simulations that the distribution of the realized factor of increase $(N_t/N_0)^{1/t}$ is approximately normal. Based on the assumption that the realized factor of increase is normally distributed, the mean and variance of $(N_t/N_0)^{1/t}$ are computed from the mean variance of N_t/N_0 by methods given in Appendices 1 and 2.

Using the formulae of Sykes (1969), the mean and variance of each age class in the future population can be computed analytically. Confidence intervals for the total population size and for the realized factor of increase, and an estimate of the probability that the future population will be larger than the starting population, are computed based on the assumption that either $\log\,(N_t/N_0)$ or $(N_t/N_0)^{1/t}$ is normally distributed.

We can also simulate the growth of an age-structured population under fluctuating environmental conditions. At each time period, a new set of fecundity and survival rates, the elements of the Leslie matrix, are chosen and used to project the population. Each fecundity and survival rate is a normally distributed random variable with specified mean, variance, and covariance with every other fecundity and survival rate. The projection, starting from the

same initial population vector, may be replicated a given number of times. From these replicated projections, the mean, variance, and covariances of the population vector are computed, together with statistics on a variety of other demographic parameters. The distributions of the final population size and the realized factor of increase are tabulated.

The computer programs to accomplish these stochastic projections are called, respectively, SPP (Stochastic Population Projection) and SLT (Stochastic Life Table simulation). Program listings and guides to the use of both programs are given in Gerrodette et al. (1983). Although lengthy, these programs are suitable for use on many microcomputers.

TABLE 1.—Initial population vector, mean vital rates, and covariance matrix of vital rates for a three age-class population projection. In the covariance matrix, *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes.

Age class	Initial population size	Mean fecundity rate	Mean survival rate	Covariance matrix						
					*F*1	*F*2	*F*3	*P*1	*P*2	*P*3
1	100	0.1	0.7	*F*1	0.0010	0.0020	0.0020	0.0005	0.0005	0.0
2	80	1.0	0.9	*F*2		0.0050	0.0045	0.0010	0.0010	0.0
3	50	0.4	0.0	*F*3			0.0050	0.0010	0.0010	0.0
	230			*P*1				0.0050	0.0045	0.0
				*P*2					0.0050	0.0
				*P*3						0.0

Numerical Examples

Two numerical examples are presented to verify various analytic results and to illustrate the use of programs SPP and SLT in a management context.

The first example is a simple artificial life table with three age classes. The mean vital rates and the covariance matrix for the vital rates are given in Table 1. This example was used to compare the predicted mean and variance in projected population size based on Sykes' (1969) formulae with the actual mean and variance from the simulation. The example was also used to test the assumption that ultimate population sizes will be lognormally distributed, and in particular whether accurate confidence limits for the tails of the distribution can be made based on this assumption.

The second example is based on a real population. A northern fur seal, *Callorhinus ursinus*, population is projected using vital rates consistent with a phase of rapid growth which occurred earlier in this century. The mean vital rates which govern the dynamics of the population are given in Table 2 (taken from Goodman 1981: table 1) and confer a population growth rate of about 8% per year. The initial age vector in this case was chosen to be the stable age distribution with a total of 100,000 females. Values for the standard deviations in vital rates in Table 2 were selected by choosing reasonable values for their coefficients of variation. Correlations in vital rates were assumed to be 0.9 between fecundities at different ages, 0.9 between survival rates at different ages, and 0.5 between all fecundities and survival rates.

TABLE 2.—Initial population vector, means, and standard deviations (S.D.) of vital rates for a fur seal population projection used as a numerical example in the text. Mean rates are taken from Goodman (1981: table 1). Each age class represents 1 yr, and only the female portion of the population is tabulated. The initial population vector is in the stable age distribution with a total of 100,000 females.

Age class	Initial population size	Mean fecundity rate	S.D.	Mean survival rate	S.D.
1	17,618	0.0000	0.0000	0.8786	0.0439
2	14,312	0.0000	0.0000	0.8786	0.0439
3	11,627	0.0050	0.0003	0.8837	0.0442
4	9,500	0.0151	0.0008	0.8888	0.0444
5	7,807	0.2631	0.0132	0.9039	0.0090
6	6,525	0.3693	0.0185	0.9191	0.0092
7	5,545	0.4250	0.0213	0.9342	0.0093
8	4,789	0.4604	0.0230	0.9443	0.0094
9	4,182	0.4756	0.0238	0.9494	0.0095
10	3,671	0.4705	0.0235	0.9443	0.0094
11	3,205	0.4655	0.0233	0.9292	0.0093
12	2,753	0.4554	0.0228	0.9039	0.0090
13	2,301	0.4402	0.0220	0.8786	0.0088
14	1,869	0.4250	0.0213	0.8484	0.0085
15	1,466	0.4048	0.0202	0.8029	0.0080
16	1,089	0.3794	0.0190	0.7524	0.0075
17	757	0.3542	0.0177	0.6918	0.0069
18	484	0.3187	0.0159	0.6262	0.0063
19	280	0.2833	0.0142	0.5454	0.0055
20	141	0.2479	0.0124	0.4494	0.0045
21	59	0.2024	0.0101	0.3282	0.0033
22	18	0.1467	0.0073	0.1009	0.0010
23	2	0.0657	0.0033	0.0000	0.0000
Total	100,000				

RESULTS

Example 1.

The results of the stochastic projection by program SPP are presented in Table 3. The second column shows the expected (mean) population vector for each time step. The mean population vector is obtained by projecting with the mean vital rates. The covariance matrix for the population vector gives, on the diagonal, the variances of each age class and, above the diagonal, the covariances between age classes.

The calculations using Sykes' formulae concur with the results of the Monte Carlo simulation of a stochastic population projection, taking the entries of the life table as time-varying random variables (program SLT). In Tables 4 and 5 the results of the simulation are presented. The means and covariances of the vital rates actually achieved on this particular run of program SLT are shown in Table 4 and are close to the specified rates given in Table 1. By comparing the results in Table 5 with those of time step 6 in Table 3, we see that the results of the simulation (SLT) and the analytic solution (SPP) agree closely.

The distribution of the ratio of the final population size to the initial population size is shown as a histogram in Figure 1A. The curve is skewed to the right,

TABLE 3.—Results of the stochastic projection of the population, given in Table 1, through 6 time steps (program SPP). The columns labeled "95% C.L." give the lower and upper 95% confidence limits for total population size and for the realized factor of increase relative to the initial population. The last column gives the probability *P* that the final population size will be greater than the initial population size.

Time step	Expected population vector	Covariance matrix			Total population			Factor of increase			*P*
					Mean	Lower 95% C.L.	Upper 95% C.L.	Mean	Lower 95% C.L.	Upper 95% C.L.	
	100										
0	80				230						
	50										
	110	142.5	18.0	14.4		215			0.934		
1	70		50.0	36.0	252	289		1.096	1.258		0.8764
	72			32.0							
	110	261.5	48.4	73.5		197			0.925		
2	77		131.0	46.1	250	307		1.041	1.156		0.7545
	83			65.3							
	113	365.3	94.4	154.1		193			0.934		
3	77		189.7	68.7	259	335		1.039	1.134		0.7856
	69			136.4							
	116	485.5	158.2	219.9		187			0.950		
4	79		244.9	99.0	264	356		1.033	1.116		0.7808
	69			184.2							
	119	559.6	230.8	287.1		184			0.957		
5	81		307.5	141.7	271	378		1.031	1.105		0.7910
	71			231.0							
	121	736.2	309.8	366.2		182			0.961		
6	83		367.0	189.7	277	400		1.029	1.096		0.7990
	73			283.5							

TABLE 4.—Means, variances, and covariances of vital rates achieved during a Monte Carlo projection of the population given in Table 1 (program SLT). Values were computed on the basis of 30,000 vectors of vital rates. *F* refers to fecundity rate, *P* to survival rate, and numbers to age classes. Values in this table should be compared with the "target" values in Table 1.

	Mean	Covariance matrix					
		*F*1	*F*2	*F*3	*P*1	*P*2	*P*3
*F*1	0.10016	0.00101	0.00202	0.00201	0.00049	0.00045	0.0000
*F*2	1.00027		0.00505	0.00453	0.00100	0.00092	0.0000
*F*3	0.39998			0.00502	0.00099	0.00091	0.0000
*P*1	0.69992				0.00501	0.00414	0.0000
*P*2	0.89744					0.00435	0.0000
*P*3	0.00000						0.0000

TABLE 5.—Results of the Monte Carlo simulation of the 6 time-step projection of the population whose age structure and vital rates are given in Table 1 (program SLT). Sample size for the simulation was 5,000 trials. Results in this table should be compared with the "predicted" values in the last row of Table 3. Here *P* is the proportion of final population sizes greater than the initial population size.

Time step	Mean population vector	Covariance matrix			Mean total population	Mean factor of increase	*P*
	121	741.3	314.7	369.8			
6	83		371.7	187.6	277	1.029	0.7954
	73			281.5			

as anticipated. Both the logarithmic transformation (Fig. 1B) and the root transformation (Fig. 1C) appear to normalize the distribution. When the cumulative frequency distributions are plotted on normal probability scales (dots in Fig. 1), however, the root transformation appears superior to the logarithmic. The dots in Figure 1C are nearly linear, indicating that the distribution is close to normal.

In Table 6 the accuracy of the 95% confidence limits for the total population size computed by the logarithmic and root transformations is compared for projections of 2, 5, and 10 time steps, using the same numerical example. Program SLT calculates the proportion of final populations which fall above and below the computed upper and lower confidence limits. We expect that 2.5% of the cases should fall above the upper limit and 2.5% below the lower limit if the 95% confidence interval has been correctly estimated. Table 6 shows that both the logarithmic and the root transformations do a fair job of estimating the 95% confidence limits. The root transformation, however, appears more accurate in this example, as well as in other examples we have tried, when the number of time steps is small. When the number of time steps is large (50-100), both transformations produce normally distributed variables.

Since the root transformation gave the most accurate results for short projections, we used this transformation in program SPP to compute a confidence interval on total population size. More details of the

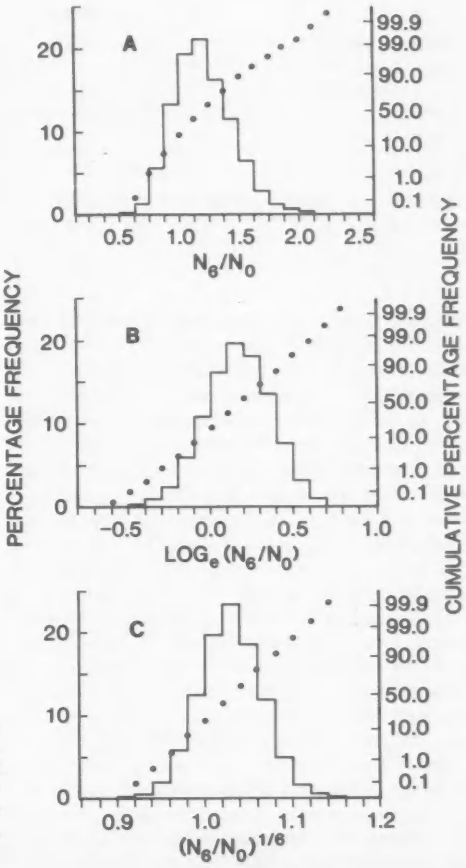

FIGURE 1.—Distributions of future total population size under variable conditions. Histograms show the percentage frequency, and dots the cumulative percentage frequency plotted on a normal probability scale, for 5,000 stochastic projections of the population given in Table 1 for six time steps. A. Distribution of N_6/N_0, the final population size divided by the initial. B. Distribution of $\log_e (N_6/N_0)$. C. Distribution of $(N_6/N_0)^{1/6}$, the realized factor of increase.

TABLE 6.—Accuracy of the 95% confidence limits (C.L.) on population size estimated by the logarithmic and root transformations of the distribution of total population size. For each transformation, the estimated lower and upper confidence limits are shown for projections of the population given in Table 1 for 2, 5, and 10 time steps. The columns labeled "Proportion beyond C.L." give the actual proportion of 10,000 stochastic projections using program SLT which fall below the estimated lower limit and above the estimated upper limit for each transformation. Each set of projections was replicated 3 times. The root transformation estimates the 95% confidence interval on population size more accurately, especially for short projections.

No. of time steps to projection		Transformation			
		Logarithmic		Root	
		Estimated 95% C.L.	Proportion beyond C.L.	Estimated 95% C.L.	Proportion beyond C.L.
2	Lower	199	0.0311	197	0.0256
			0.0317		0.0255
			0.0295		0.0231
	Upper	309	0.0160	307	0.0204
			0.0181		0.0214
			0.0199		0.0228
5	Lower	187	0.0290	184	0.0251
			0.0285		0.0242
			0.0318		0.0260
	Upper	380	0.0227	378	0.0245
			0.0219		0.0235
			0.0215		0.0235
10	Lower	178	0.0266	175	0.0238
			0.0280		0.0252
			0.0286		0.0257
	Upper	489	0.0226	486	0.0234
			0.0211		0.0221
			0.0217		0.0226

example projection are shown in the columns on the right side of Table 3. The mean and the 95% confidence interval for the total population size and for the realized factor of increase are given for each time step. As the population vector approaches the stable age distribution, the ratio between successive mean total population sizes approaches the asymptotic value 1.0240. The mean realized factor of increase shown in Table 3, which is computed relative to the initial population, does not converge on this asymptotic value; nor can the mean realized factor of increase be computed from the ratio of the mean final population size to the initial population size. Instead, the mean and variance of the realized factor of increase are computed by methods described above.

The probability that the total population size will have increased over its initial value is also shown for each time step in the last column of Table 3. In this particular example, since we did not begin with the stable age distribution, this probability decreases at first and then increases. As a further check, program SLT computes the proportion of cases in which the final population was greater than the initial population, and this answer (0.7954, Table 5) is close to the probability computed analytically by program SPP assuming that the realized factor of increase is normally distributed (0.7990, Table 3). Given a population whose age structure and dynamics conform to the values given in Table 1, therefore, we can make the statement that there is an 80% chance that the population will be larger 6 time steps from now and a 20% chance that it will be smaller.

Example 2.

The results of the stochastic projection of the northern fur seal population by program SPP are given in Table 7 and Figure 2. Table 7 shows that after 5 yr, the expected (mean) number of 9-yr-olds, for example, is 6,188 with a standard deviation of 333. The expected total population size is 147,982 with a standard deviation of 8,832. The mean and standard deviation of the realized factor of increase are 1.0812 and 0.0129, respectively; from these values we compute the 99% confidence interval on population size to be from 126,410 to 171,930. Note

TABLE 7.—Results of the 5-yr stochastic projection of the northern fur seal population, based on the age structure and vital rates given in Table 2. Probability that the final population > initial population = 0.999+.

Age class	Expected population size	Standard deviation
1	26,071	1,672
2	21,179	1,619
3	17,205	1,519
4	14,058	1,402
5	11,553	1,280
6	9,655	972
7	8,205	720
8	7,087	516
9	6,188	333
10	5,432	121
11	4,743	106
12	4,075	92
13	3,406	76
14	2,767	62
15	2,170	49
16	1,611	36
17	1,121	25
18	717	16
19	415	9
20	209	5
21	87	2
22	26	1
23	2	0.05
Total	147,982	

	Total population	Factor of increase
Lower 99% C.L.	126,410	1.0480
Expected value (mean)	147,982	1.0812
Upper 99% C.L.	171,930	1.1145

that, as will generally be the case, the confidence interval for total population size is not symmetric about the mean value.

In the last line of Table 7, the probability of an increased population is shown to be very close to 1.0. In other words, it is virtually certain that the population will have increased in size after 5 yr. Figure 2 presents the results for total population size graphically. The 95% and 99% confidence limits computed by program SPP are shown for each time step. The confidence limits grow nearly geometrically.

DISCUSSION

Fishery and wildlife management often involves predictions of population size, and, owing to imperfect knowledge of the world, these predictions are uncertain. Accordingly, a practical analysis attaches estimates of confidence intervals for any given prediction. The programs described in this paper carry out the computation of confidence intervals for projections of age-structured populations, if we can specify the statistics of the variation in the age-specific vital rates. Realistically, we do not expect there to be be many examples where the statistics of the variation in vital rates are genuinely known with substantial precision, for these rates are difficult to measure in natural populations. Nevertheless, in an imperfect world, management decisions must be made with imperfect data. A considerable component of the uncertainty in a population prediction will be owing to the phenomena treated in this paper. Thus, even the use of very rough guesses at the statistics of the variation in the age-specific vital rates, in order to estimate confidence intervals in a population projection, is preferable to neglecting this source of variation entirely. At the very least, incorporation of speculative estimates in this applied context will allow the exploration of "what if" questions in a fashion that can indicate priorities for future data gathering.

In many fish and aquatic invertebrate species, there is an enormous variation in the success of year classes. In such cases the population dynamics may be dominated by the overwhelming abundance of one

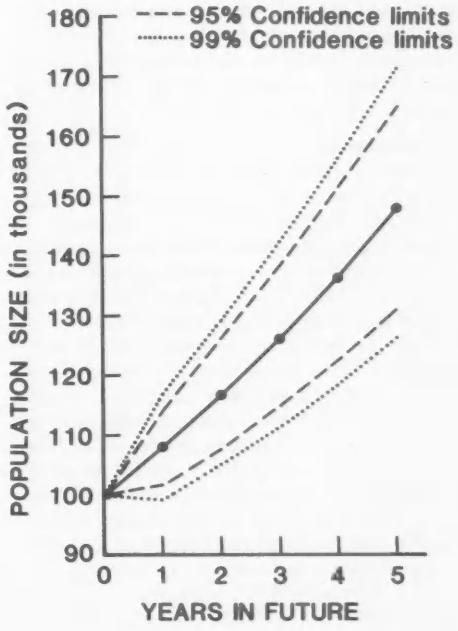

FIGURE 2.—Confidence limits for future total female population size for the northern fur seal, based on the schedule of vital rates in Table 2. The solid line plots the mean population trajectory.

or two cohorts. The environmental factors which lead to such huge variations in recruitment are as yet imperfectly understood for most species. In order to predict future population sizes, the year-to-year variation could be incorporated into the variances of the effective fecundity terms in the first row of the Leslie matrix. This will lead to enormous (but realistic) confidence limits for predicted future population sizes of such stocks. A more fruitful use of the results of this paper, however, would be to separate recruitment uncertainty from survival uncertainty and to calculate a confidence interval on future population size given recruitment success for a particular cohort. Among harvested species such a conditional forecast could be used to incorporate environmental variation into management recommendations.

In keeping with the fact that applied management may often depend on very elementary quantities, we also calculate a particularly important special statistic of the distribution of projections – the probability that the population will increase under the specified conditions. In the first example, the probability of an increased population was found to be about 0.8. In the second example, the fur seal population projection, there is a higher probability that the population will increase. Starting with the female population of 100,000, the calculations indicate 99% certainty that the population will have increased to between 126,410 and 171,930 in 5 yr.

Our simulations of stochastic population growth differ from previous efforts by Boyce (1977) and Slade and Levenson (1982) by allowing all vital rates to vary simultaneously, rather than only one at a time, and by permitting correlations among the vital rates to be specified. In the stochastic growth models of Cohen (1977, 1979a) and Tuljapurkar and Orzack (1980), at each time step the population finds itself in one of several possible environments. Within each environment vital rates are fixed. By contrast, here we model a single variable environment whose conditions, as reflected in the population's vital rates at any point in time, are never precisely duplicated. The results of Example 1 verify the results for the mean and variance of future population vectors and show that the mean and variance for total ultimate population size can be computed from Sykes' formulae. Our results confirm the conclusions of Cohen (1977), Tuljapurkar and Orzack (1980), and Slade and Levenson (1982) that the expected mean value of a stochastic population projection with no serial correlation in vital rates is equivalent to the value projected deterministically from mean vital rates. Cohen (1979a, b) and Tuljapurkar (1982) address the more general question of serial correlation in vital rates.

All of the work cited above has been concerned with the state of the population at a time in the future much greater than will generally be useful in management. In this paper we have examined the stochastic behavior of the population at a shorter time in the future. Example 1 has verified that the distribution of ultimate population sizes from stochastic population projections is approximately lognormal (Tuljapurkar and Orzack 1980). From the perspective of fitting the tails of this distribution for a small number of time steps t, however, it appears better to assume that the $1/t$th power of the distribution is normally distributed. In either case the distribution of ultimate population sizes is skewed (with long tails at the higher values), and the skew becomes more pronounced as t increases. An important property of such a distribution is that the most likely or modal population value will always be smaller than the mean. How much smaller depends on the number of time steps t, and on the variances and covariances among the survival and fecundity rates.

An interesting theoretical and practical problem is to find a descriptor of population growth under stochastic conditions which characterizes the skewed distribution of ultimate population size. Cohen (1979a) has proposed two measures of long-run population growth: λ, the ensemble average of realized factors of increase; and μ, the factor of increase needed to realize the ensemble average of final population sizes. The first is a measure based on growth rates, while the second is based on population sizes (Cohen 1979b). The average realized factor of increase calculated here is analogous to λ. If the Leslie matrix of mean vital rates is known, μ is easily calculated as the dominant eigenvalue of that matrix. The problem, as we have seen, is that under stochastic conditions the mean of the population sizes is not very informative and may, in fact, be misleading. Tuljapurkar (1982) has proposed a growth measure α which leads to the approximate median population size. The two measures proposed here – namely, $E[(N_t/N_0)^{1/t}]$ and $E[\log(N_t/N_0)]$ – are close approximations to the rate of growth leading to the modal population size. As such, they may loosely be said to describe the most probable trajectory of the population under stochastic conditions.

ACKNOWLEDGMENTS

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APPENDIX 1.

Calculation of the mean and variance of the realized factor of increase, assuming it is normally distributed.

Let λ, the realized factor of increase, be defined as the tth root of the ratio of the population size at time t to the initial population size:

$$\lambda = \left(\frac{N_t}{N_0}\right)^{1/t}$$

or

$$\lambda^t = \frac{N_t}{N_0}$$

Let μ be the mean and ν the variance of λ. The mean and variance of λ^t are given by formulae in the Methods section. The problem is to find the mean and variance of λ.

Let $F(\mu,\nu)$ be a function which gives the tth moment of λ:

$$F(\mu,\nu) = E(\lambda^t).$$

Similarly let $G(\mu,\nu)$ be a function which gives the variance of λ^t in terms of the tth and $2t$th moments of λ:

$$G(\mu,\nu) = E(\lambda^{2t}) - [E(\lambda^t)]^2.$$

Now assume that λ is normally distributed. Appendix 2 gives a recursive algorithm which allows any moment of a normally distributed variate to be calculated. From the tth and $2t$th moments of λ, the functions F and G can be computed from the equations above. Generally, F and G will be tth and $2t$th order polynomials in μ and ν. Then, with F and G known, we have a system of two equations

$$F(\mu,\nu) - E(\lambda^t) = 0$$
$$G(\mu,\nu) - \mathrm{Var}(\lambda^t) = 0$$

in two unknowns. Given initial estimates of μ and ν, a two-variable version of Newton's method, or any similar iterative technique, can be used to converge on a simultaneous solution.

APPENDIX 2.

A recursive algorithm for computing the higher order moments of the normal distribution.

The moment generating function for the normal distribution is

$$M_x(t) = e^{\mu t + \frac{\nu t^2}{2}}$$

where μ is the mean and ν is the variance of the normal variate x. The nth moment of x is found by evaluating, at $t = 0$, the nth derivative of $M_x(t)$ with respect to t. The nth differentiation with respect to t leads to the series

$$(\mu + \nu t)^n M_x(t) + \ldots + A(\mu + \nu t)^\alpha \nu^\beta M_x(t) + B(\mu + \nu t)^{\alpha-2} \nu^{\beta+1} M_x(t) + \ldots,$$

which, evaluated at $t = 0$, gives

$$\mu^n + \ldots + A\mu^\alpha \nu^\beta + B\mu^{\alpha-2} \nu^{\beta+1} + \ldots,$$

where A and B are coefficients and α and β are exponents such that $\alpha + 2\beta = n$. The next [$(n + 1)$th] differentiation of the middle terms gives

$$\begin{aligned} &A(\mu + \nu t)^{\alpha+1} \nu^\beta M_x(t) + A\alpha(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) \\ &+ B(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) + B(\alpha - 2)(\mu + \nu t)^{\alpha-3} \nu^{\beta+2} M_x(t) \\ &= \ldots + (A\alpha + B)(\mu + \nu t)^{\alpha-1} \nu^{\beta+1} M_x(t) + \ldots \end{aligned}$$

which, evaluated at $t = 0$, gives

$$\ldots + (A\alpha + B)\mu^{\alpha-1} \nu^{\beta+1} + \ldots.$$

Thus the coefficient of each term of the series of the $(n + 1)$th moment can be computed from the two terms in the series of the nth moment "before" and "after" it. The exponents of μ and ν follow the regular pattern shown.

LIFE HISTORY CHARACTERISTICS OF *PANDALUS MONTAGUI* AND *DICHELOPANDALUS LEPTOCERUS* IN PENOBSCOT BAY, MAINE

DAVID K. STEVENSON[1] AND FRAN PIERCE[2]

ABSTRACT

A number of life history characteristics of two species of pandalid shrimp from Penobscot Bay, ME, were inferred from length-frequency and relative abundance data collected on five occasions during a bottom trawl survey in 1980-81. *Pandalus montagui* is a sequential hermaphrodite. Sex transition occurs throughout the year, but most transitional individuals were observed in late March. Most individuals change sex shortly before or after reaching age 2, but some do so either a year earlier or a year later. Ovigerous females were observed from late November through January; eggs are apparently produced during the second, third, and fourth years. Fifteen percent of the 0 age-group caught in the fall of 1980 were females which may never have functioned as males. Growth was rapid in the spring and summer and negligible in the late fall and winter. Females which changed sex at age 1 were larger than females which changed sex a year later. *Dichelopandalus leptocerus* is not hermaphroditic. Ovigerous females were collected primarily in late November and early December. Some females produce eggs during their first and second years, but most do so only during their second year. None of the females caught during this study appeared to be older than age 2; a few large males remained in the population during their third year of life. Females of both species were larger than males of the same age-group, a distinction which was attributed to differences in growth rate and, for *P. montagui*, was associated with earlier sex transition. Larger shrimp of both species migrated down the Bay into deeper water as the winter progressed.

The Pandalidae are a family of boreal, subarctic shrimp composed of 2 genera and about 20 species. Four species (*Pandalus borealis*, *P. montagui*, *P. propinquus*, and *Dichelopandalus leptocerus*) are common in offshore waters of the Gulf of Maine (Wigley 1960). Of these, *P. borealis* is the largest, reaching a maximum total length of 17-18 cm (7 in), and has been the object of a directed winter fishery in coastal waters of the Gulf of Maine since the late 1930s (Scattergood 1952) and in coastal and offshore waters since 1958[3]. This species is also exploited commercially on the west coast of North America, in the Canadian Maritime Provinces, on the west coast of Greenland, in the Norwegian and North Seas, and in the northwest Pacific (Balsiger 1981).

Pandalus montagui and *D. leptocerus* are smaller species (maximum length 10 cm or 4 in), which are harvested incidentally with *P. borealis* in the Gulf of Maine, but have little or no market value because of their size. *Pandalus montagui* is also harvested as an incidental species in the Gulf of St. Lawrence (Balsiger 1981), and for many years was the object of several localized commercial beam trawl fisheries in the southern North Sea and in Morecambe Bay, northwest England, until declining stock sizes led to the demise of the fisheries in the Thames estuary (described by Mistakidis 1957) and Morecambe Bay in the 1950s and 1960s. Warren (1973) described a fishery for *P. montagui* in the Wash on the east coast of England which was still active in the early 1970s. *Pandalus propinquus* is also smaller than *P. borealis* and is generally restricted to deeper water (165-330 m in New England waters according to Wigley 1960); consequently it is rarely taken in Gulf of Maine commercial catches.

Pandalus montagui is differentiated taxonomically into two subspecies: *P. montagui tridens* in the North Pacific and *P. montagui montagui* in the North Atlantic from the Arctic south to the British Isles and Cape Cod (Simpson et al. 1970) or Rhode Island (Rathbun 1929). According to Simpson et al. *P. montagui montagui* is found in estuaries, coastal waters, and offshore in depths of 5 to over 700 m, but is more common in shallow waters (20-90 m); at depths > 90 m it is gradually replaced by *P. borealis*.

[1]Zoology Department, University of Maine, Orono, ME 04469 and Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[2]Maine Department of Marine Resources, West Boothbay Harbor, ME 04575.

[3]Stickney, A. P. 1980. A characterization of the northern shrimp fishery of Maine. *In* C. J. Walton (editor), Fisheries management and development, Vol. III, Element D: Characterization of the shellfisheries, p. 244-293. Completion report to the State Planning Office, Oct. 1, 1978-Sept. 30, 1979, Maine Department of Marine Resources, Augusta.

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Squires (1968) reported that *P. borealis* occurred together with *P. montagui* in depths < 200 m in the Gulf of St. Lawrence and southwest of Newfoundland, but at depths between 200 and 300 m with a smooth detritus bottom and temperatures of 4°-6°C, only *P. borealis* were caught; in colder temperatures (−1° to 3°C) in this same depth range, *P. montagui* were more abundant. *Pandalus montagui* was described as a more eurythermal and eurybathic species than *P. borealis*. Of all the pandalids in the northwest Atlantic, *P. montagui* is the only one which inhabits colder Arctic waters < 1.5°C (Squires 1966). The Atlantic subspecies of *P. montagui* has been the subject of several biological studies (Mistakidis 1957; Allen 1963; Couture and Trudel 1969a, b).

Dichelopandalus leptocerus is distributed in the northwest Atlantic from Newfoundland to North Carolina (Rathbun 1929). It has not been reported from the northeast Atlantic and is rare in the northern Pacific (Squires 1966). During a November 1956 bottom trawl survey in New England waters, *D. leptocerus* was much more widely distributed than *P. montagui* or *P. borealis* (Wigley 1960). *Dichelopandalus leptocerus* was also found over a broad depth range (33-340 m), but was common between 35 and 145 m and at temperatures (in November) of 5°-20°C, whereas *P. montagui* occurred primarily between 70 and 135 m and at temperatures of 6°-10°C. *Dichelopandalus leptocerus* was also collected in areas where bottom sediments contained low, medium, and high quantities of organic matter, whereas *P. montagui* appeared to be associated with sediments with relatively low organic content. Thus, in several ways, *D. leptocerus* appears to have less restricted habitat requirements than *P. montagui* (or *P. borealis*). No detailed biological studies of *D. leptocerus* have been published.

The Maine Department of Marine Resources conducted an exploratory bottom trawl survey to determine the abundance and distribution of pandalid shrimp populations in Penobscot Bay (Figure. 1) during 1980-81. During the course of this survey, biological data were collected from about 10,000 shrimp. The objective of this paper is to describe important life history characteristics of *P. montagui* and *D. leptocerus* in Penobscot Bay (the Bay); these include breeding seasons, female sizes and ages at maturity, sex transition, growth, longevity, and migratory behavior. Aspects of the life cycle and reproductive biology of each species were examined as functions of time of year, depth, and location within the Bay.

METHODS

The survey was conducted over the course of a 12-mo period from late November 1980 to early October 1981. Samples were collected during five distinct periods of time at 19 different stations located from Cape Jellison in the northern end of Penobscot Bay to Mark Island, a distance of about 37 km (23 mi) (Fig. 1). Stations were established at depths ranging from 12 m (40 ft) to 84 m (280 ft) and were located in areas of trawlable bottom. Since a primary objective of the survey was to stimulate commercial shrimp fishing, no attempt was made to randomly select station locations, depths, or sampling times. Attempts were made, however, to return to each station as often as possible so as to determine the seasonal variation in the relative abundance of different sexes, reproductive stages, and size groups of each species at individual locations over the course of the year. Adjacent, well-defined, length groups were assumed to represent successive age-groups.

A total of 45 successful tows (i.e., tows that were not aborted because of bottom obstructions, damage to the trawl, or gear malfunction) were made during the entire survey. Of these, 37 tows which could be assigned to a specific area, depth range, and sampling period were selected for data analysis. Area 1 was defined as the upper Bay, area 2 as west of Islesboro, area 3 as south of Islesboro, and area 4 as east of Islesboro; depth ranges were defined as shallow (12-25 m), moderate (25-50 m), and deep (50-85 m) (Table 1). The distributions of sampling effort between stations by sampling period, area, and depth range are shown in Table 2. No data were

TABLE 1.—Definitions of coded sampling periods, areas, and depth ranges, 1980-81 Penobscot Bay shrimp survey.

Sampling periods	
1	20 November-2 December 1980
2	21-29 January 1981
3	24-31 March 1981
4	16 July-18 September 1981
5	5-6 October 1981
Areas	
1	Upper Bay: stations 2, 3, 4, 6, 18
2	West of Islesboro: stations 1, 5, 9, 10, 14
3	South of Islesboro: stations 7, 8, 12, 15, 16, 17, 19
4	East of Islesboro: stations 11, 13
Depth ranges	
1	12-15 m (shallow)
2	25-50 m (moderate)
3	50-85 m (deep)

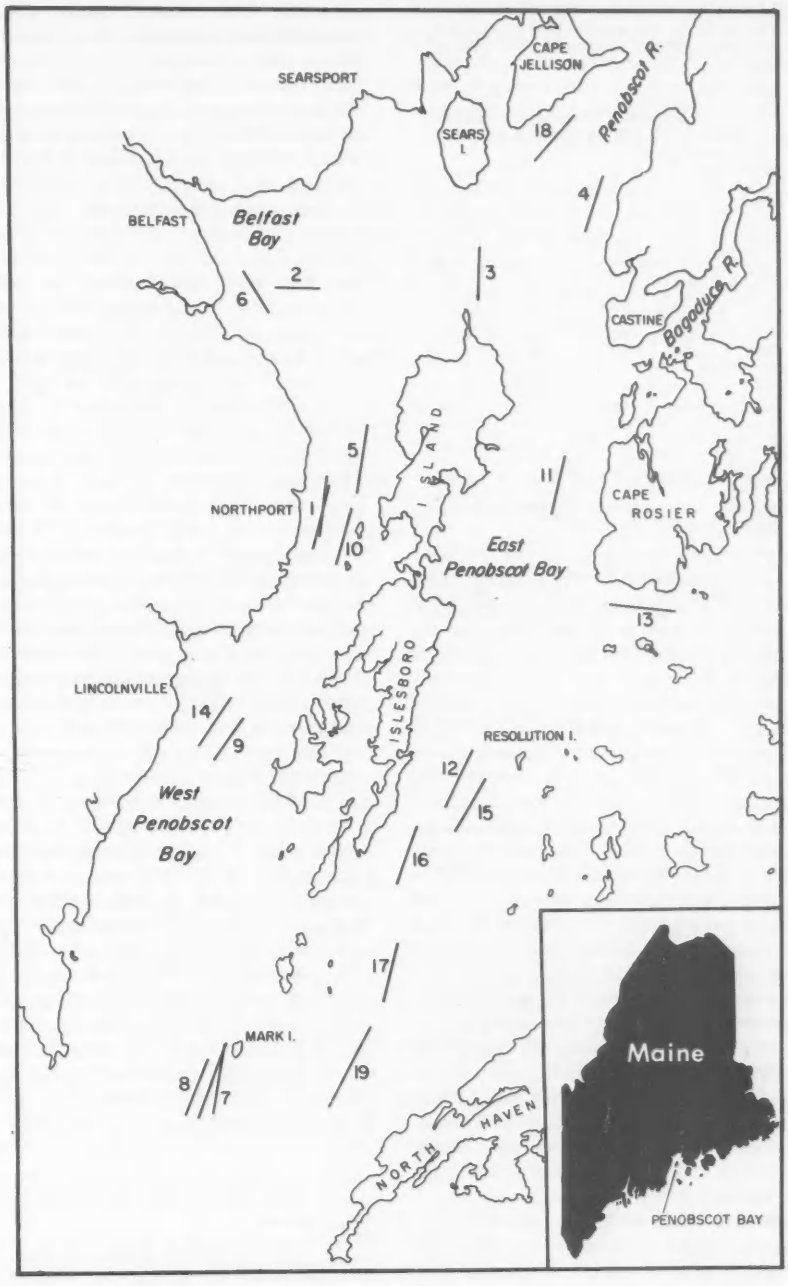


FIGURE 1.–Map of Penobscot Bay, ME, showing bottom trawl stations visited during 1980-81 survey.

TABLE 2.—Distribution of sampling effort (number of tows per station) by sampling period, area, and depth range, 1980-81 Penobscot Bay shrimp survey.[1]

	Sampling period					Area				Depth		
Station	1	2	3	4	5	1	2	3	4	1	2	3
1	2	1		6			9				9	
3	1		1			2				2		
4	1					1				1		
5	1						1				1	
6	1					1				1		
7		1	1		1			3				3
8	1							1				1
9	1		1				2				1	1
10	1	1	3				5				5	
11			1		1				2		1	1
12		1						1				1
13		1							1			1
15		1						1				1
16		1	1		1			3				3
17		1						1				1
18		2				2				2		
19			1					1				1
Totals	9	10	9	6	3	6	17	11	3	6	17	14

[1]See Table 1 for definitions of coded sampling periods, areas, and depth ranges.

available from stations 2 and 14. Trawling operations were limited to the area between Northport and Islesboro in the summer of 1981, since the only vessel available at that time was not equipped to work elsewhere in the Bay.

The trawl used was a semiballoon shrimp try-net with a 7.6 m (25 ft) headrope and 9.5 m (31 ft) footrope with no rollers; mesh size was 38 mm (1½ in) in the body and 31 mm (1¼ in) in the cod end. The trawl was also equipped with a 12.5 mm (½ in) liner. The net was rigged on 1.2 m (4 ft) legs with ark floats on the headrope and 2/0 chain on the footrope. The trawl doors were hardwood, 76 × 41 cm (30 × 16 in), with iron bracings and a wide shoe. The net was fished on a single trawl wire attached to a 30.5 m (100 ft) wire net bridle. All tows lasted 30 min and were made at speeds varying from 1.5 to 2.5 kn. Loran bearings were recorded at the beginning and end of each tow, and depth was recorded either as a single reading or at the beginning and end of each tow. Location and depth could not be determined in the summer since the vessel used then did not have sonar or navigational equipment. Although three different vessels were used during the course of the survey, the gear was identical and was fished the same way during the entire survey.

If catches were small (under 1 kg), the entire catch was generally brought to the laboratory and frozen for later analysis; otherwise, the catch was subsampled aboard the vessel. In some cases, large samples were further subsampled in the laboratory after they were thawed. Inasmuch as was possible, all samples and subsamples were randomly selected. Samples (or subsamples) of 200-900 g were sorted (after removing extraneous "trash") by species according to morphological characteristics described by Rathbun (1929). Biological data were compiled for a total of 7,259 *D. leptocerus* and 2,475 *P. montagui*; numbers of *P. borealis* were inadequate for data analysis. Each individual shrimp was sexed (male, female, or transitional) using external morphological characteristics for the genus *Pandalus* originally described by Wollebaek (1908), Berkeley (1930), Jägersten (1936), and Leloup (1936) and summarized by Mistakidis (1957). The females were further grouped as ovigerous or non-ovigerous depending on whether or not the eggs had "dropped" and were being carried on the pleopods; the non-ovigerous females were further subdivided into two groups—those which had never carried eggs before and those which had—based on the presence or absence of sternal spines. This characteristic of non-ovigerous females was originally described by McCrary (1971) for three pandalid species (*Pandalus borealis*, *P. goniurus*, and *P. hypsinotus*) in Alaska. Stage I females were defined as those which had not carried eggs before and Stage II females as those which had; there was no way to distinguish between females which had carried eggs only once before and those which had carried eggs more than once. Carapace lengths were measured between the eye socket and posterior dorsal edge of the carapace and recorded to the nearest 0.1 mm.

For each species, the numbers and lengths of shrimp in each biological category (sex, with or without eggs, Stage I or II) were compiled by sampling period, geographic area, and depth range. Length frequencies were expressed as numbers of shrimp per 0.5 mm dorsal carapace length. Since nearly all of the samples collected in areas 1-3 were also collected in specific depth ranges (i.e., all 6 samples from area 1 were from shallow water, 16/17 samples from area 2 were from moderate depths, and all samples from area 3 were from deep water), length frequencies were presented for appropriate area/depth combinations. Length-frequency data for *P. montagui* collected in October 1981 were not presented since so few individuals were captured.

RESULTS AND DISCUSSION

Breeding Seasons and Female Sizes (Ages) at Maturity[4]

Nearly all the ovigerous female *D. leptocerus* were

caught in November-December 1980 (Table 3), although a few remained in January and March. It was therefore apparent that most eggs hatched during a relatively short period of time in late December and early January. Although only the larger size group was carrying eggs (Fig. 2D), the presence of a few Stage II non-ovigerous females in roughly the same size range (Fig. 2C) indicated that some females produced eggs a year earlier as well. It could not be determined from the samples collected during this study whether the younger females spawned earlier or later than the older group. The fact that so few Stage II females were captured in the Bay at any time of year indicated that most of the spawning population was made up of first time spawners. Ovigerous females were collected at all depths and in all areas (Tables 4, 5), but made up a greater percentage of the catch at moderate depths in area 2.

Nearly all of the ovigerous female *P. montagui* were collected in November-December and late January (Table 6); the fact that 50% of the females in late January were still ovigerous suggests that eggs hatched over a more prolonged period then was true for *D. leptocerus*, possibly from November at least through February. Females belonging to two North Sea *P. montagui* populations were reported to carry eggs primarily between November and February (Mistakidis 1957; Allen 1963), although ovigerous females were observed from mid-October to April in the Thames estuary by Mistakidis. Hatching times were reported for the same populations as late February through April with peak activity in April. According to Couture and Trudel (1969b), ovigerous females were observed in Grand-Rivière, Quebec, beginning in July and accounted for the greatest percentage of the population in October (no samples

TABLE 3.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	49.7	65.3	59.4	47.6	53.0	53.2
Females/Stage I	32.0	33.5	37.8	50.2	45.3	38.8
Females/Stage II	1.4	0.3	1.5	2.2	1.5	1.5
Total non-ovigerous females	33.4	33.7	39.3	52.4	46.8	40.2
Ovigerous females	16.8	1.0	1.3	0.0	0.2	6.6
Total females	50.3	34.7	40.6	52.4	47.0	46.8
Total no. individuals	2,694	729	1,151	1,107	1,577	7,259

TABLE 4.—Percent total number of male and female *Dichelopandalus leptocerus* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	54.4	49.3	57.4	70.6	53.0
Females/Stage I	42.2	39.7	36.7	26.1	38.9
Females/Stage II	1.0	1.8	1.1	1.1	1.4
Total non-ovigerous females	43.2	41.5	37.8	27.2	40.3
Ovigerous females	2.4	9.2	4.8	2.2	6.6
Total females	45.6	50.7	42.6	29.4	47.0
Total no. individuals	1,047	3,626	2,419	92	7,184

TABLE 5.—Percent total number of male and female *Dichelopandalus leptocerus* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	54.4	47.7	60.3	53.3
Females/Stage I	41.5	40.4	32.4	37.6
Females/Stage II	1.1	2.0	0.9	1.4
Total non-ovigerous females	42.6	42.4	33.3	39.0
Ovigerous females	3.0	9.9	6.4	7.7
Total females	45.6	52.3	39.7	46.7
Total no. individuals	812	3,015	2,299	6,126

[4]Since no internal sexual characteristics (such as oocyte development) were examined in this study, the breeding season was defined as the period of time when ovigerous females were observed and sizes (ages) at maturity as the sizes (ages) when females produce eggs. No comparable information for males (i.e., mating times or sizes (ages) at maturity) was available. As used in this paper, the breeding season was, strictly speaking, the period of time between spawning and hatching when eggs were incubated.

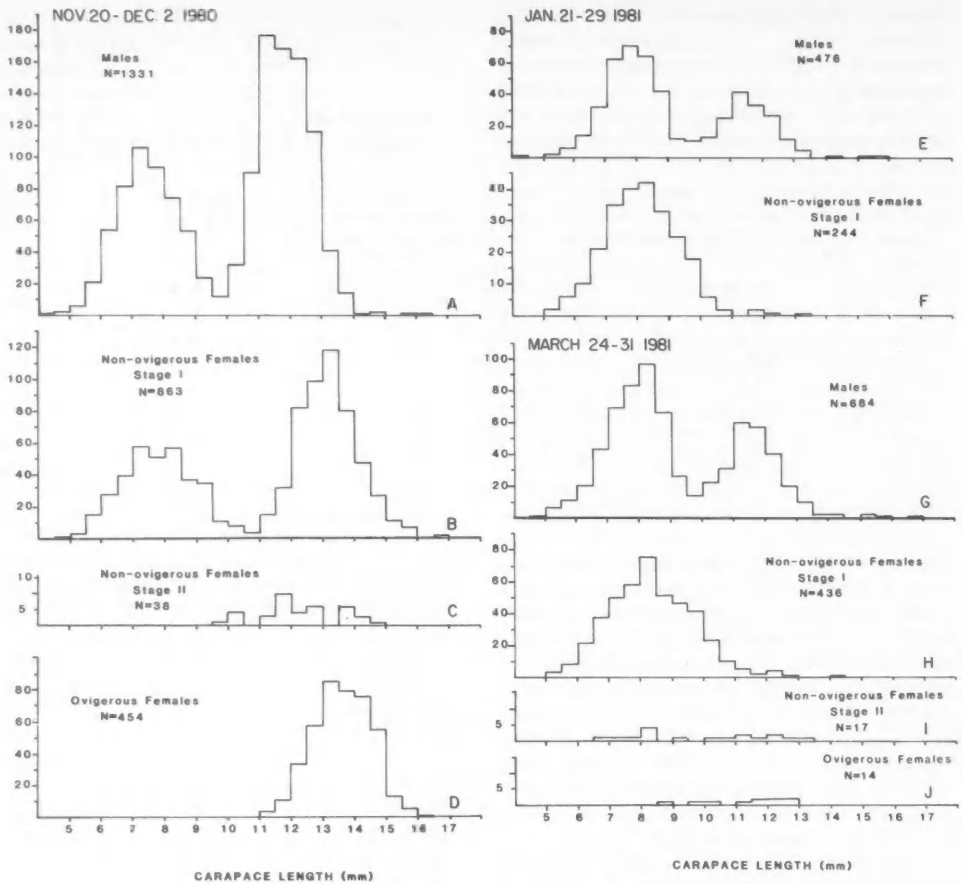
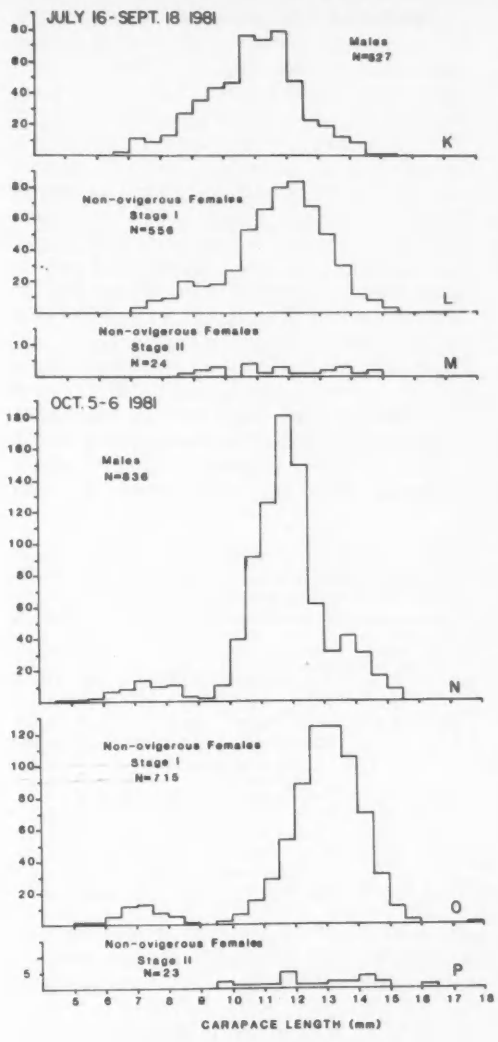


FIGURE 2.—*Dichelopandalus leptocerus* numerical length-frequency distributions by sex and reproductive stage.

TABLE 6.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all locations and depths in Penobscot Bay during five sampling periods in 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	11/20-12/2 1980	1/21-1/29 1981	3/24-3/31 1981	7/16-9/18 1981	10/5-10/6 1981	Total
Total males	73.2	85.2	68.4	37.3	34.3	68.9
Transitionals	0.3	2.5	15.4	5.7	1.5	6.9
Females/Stage I	7.8	6.1	15.9	50.4	61.2	18.2
Females/Stage II	0.3	0.0	0.0	6.7	3.0	1.2
Total non-ovigerous females	8.1	6.1	15.9	57.0	64.2	19.4
Ovigerous females	18.4	6.2	0.4	0.0	0.0	4.8
Total females	26.5	12.3	16.2	57.0	64.2	24.2
Total no. individuals	332	871	800	405	67	2,475



were collected between November and April). A few females were still carrying eggs the following June. Hatching began in the winter and continued through June. *Pandalus montagui* populations studied in Penobscot Bay and Grand-Rivière spawned primarily in their second and third years. Females in the North Sea, on the other hand, were fully mature during their first year (Mistakidis 1957; Allen 1963), but there was no evidence that individual age-groups spawned more often there than at Grand-Rivière or in Penobscot Bay.

At least two age-groups of ovigerous *P. montagui* were apparent in the winter samples (Fig. 3C, G), whereas only a single age-group of ovigerous *D. leptocerus* was observed (Fig. 2D). Length-frequency data suggested that older female *P. montagui* (age 2+) spawned before younger females (age 1); 57% of the ovigerous females collected in November-December were > 15 mm CL (Fig. 3C), whereas only 30% remained in the same size group in late January (Fig. 3G). Sample sizes were much too small, however, to clearly indicate how many spawning age-groups were present or whether older females spawned earlier than younger ones. Earlier completion of spawning by older females was reported by Mistakidis (1957) in the Thames estuary. In Penobscot Bay, the relative abundance of ovigerous females was higher in moderate and deep waters and in areas 2, 3, and 4 (Tables 5, 6).

The capture of a single 10 mm CL ovigerous female *P. montagui* in January (Fig. 3G) indicates that a few females mature and reproduce during their first year. This shrimp could have started life as a female or could have changed sex in the first year and therefore never functioned sexually as a male. Mistakidis (1957) reported that some 0 age-group males in the Thames estuary changed sex and functioned as females during their first year. Some individuals in both the Thames estuary and Northumberland began life as females and matured in their first year (Mistakidis 1957; Allen 1963).

Sex Transition

Unlike most other Pandalid species, the Penobscot Bay population of *D. leptocerus* was not hermaphroditic. Not a single transitional individual was identified in the over 7,000 shrimp which were examined. Furthermore, males and females recruited to the > 5 mm CL population in October of their first year in nearly equal numbers (Fig. 2N, P). The ratio of males to females for the entire survey period was 53:47 (Table 3). *Pandalus montagui*, on the other hand, is a protandric (sequential) hermaphrodite. Nearly 7% of the 2,475 individuals examined exhibited external morphological characteristics typical of transitional *P. borealis* (Allen 1959). The sex ratio was 69% males to 7% transitionals to 24% females (Table 6). Although *P. montagui* is clearly protandric, some individuals in Penobscot Bay either begin life as females or assume external female characteristics by late November of their first year.[5] These

[5]Individuals of protandric pandalid shrimp species which begin life as females are referred to as primary females; those which change

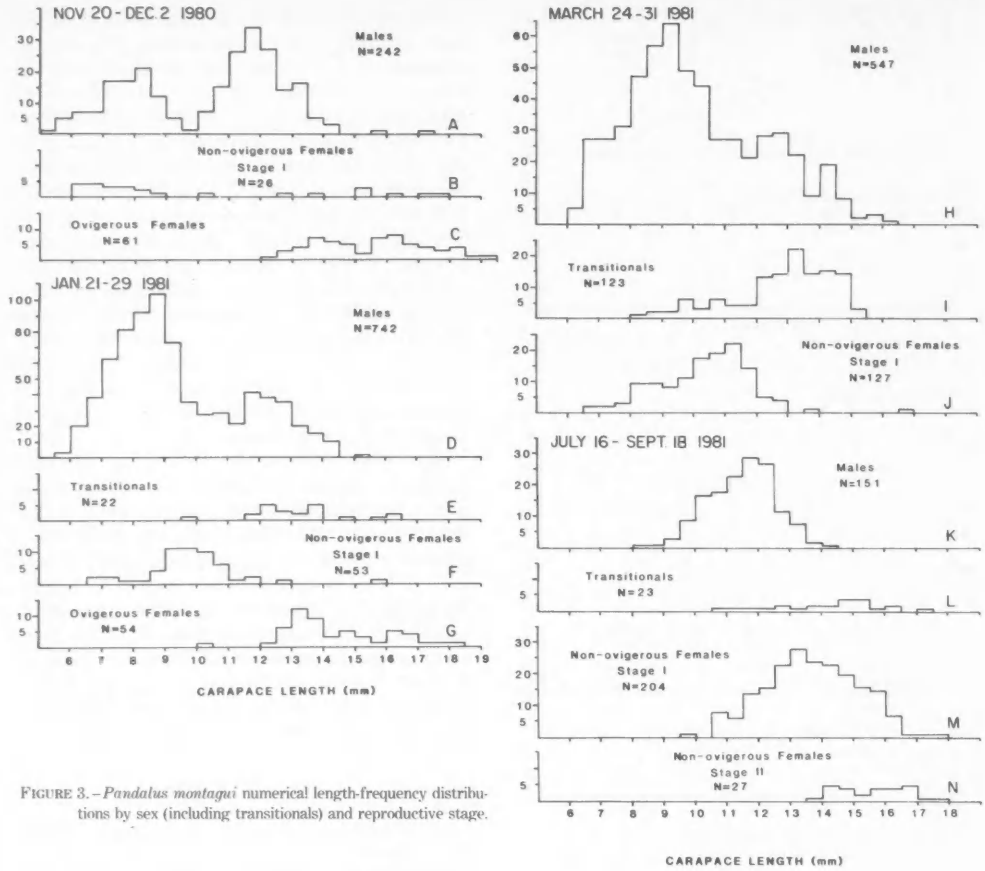


FIGURE 3.—*Pandalus montagui* numerical length-frequency distributions by sex (including transitionals) and reproductive stage.

females were obvious as a distinct size-group in the November-December length-frequency data at 6-9 mm CL (Fig. 3B). At this time, these females made up 15% of the newly recruiting 0 age-group. The relative abundance of 0 age-group females was considerably higher in the North Sea: 29-37% of most samples in the Thames (Mistakidis 1957) and about 50% in Northumberland (Allen 1963). On the other hand, only 11.2% of the age-1 *P. montagui* collected in May 1965 in Grand-Rivière were females (Couture and Trudel 1969b).

Size (Age) at Sex Transition

Transitional *P. montagui* were collected during all five sampling periods, but were most abundant in late March (Table 6) following the end of the breeding period. Sex transition apparently began in January, peaked in late March, and continued through the summer and early fall, reaching a minimum in late November. The rapid decline in the relative abundance of males after January 1981 and the accompanying increase in females after March (Table 6) indicated that shrimp, which functioned as males in the previous breeding season and became

sex in their first year following the repression of male sex characteristics and never function as males are called secondary females; and those which function first as males and then change sex are called hermaphroditic females (Mistakidis 1957). Since no distinction could be made in this study between the three types of female *P. montagui*, we have avoided the use of this terminology altogether and simply distinguish between individuals which remained as males during their first year, those which were females when they were first captured in November-December of their first year, and those which apparently changed sex during their first winter.

females prior to the subsequent breeding season, assumed external female characteristics during the winter and spring. The appearance of a distinct size-group of 9-11 mm CL females in late January (Fig. 3F) which was not present 2 mo earlier (Fig. 3B), suggests that transition was well underway by late January. The two size-groups of non-ovigerous females in January and March (Fig. 3I) were assumed to belong to the same age-group, the smaller females being those which did not function as males in their first year (they may have started life as females) and the larger females being those which were still males in November-December (Fig. 3A). Transitional shrimp made up a larger percentage of samples collected in moderate and deep waters and in areas 3 and 4 (Tables 7, 8).

Transition of the younger age-group which was first captured in November-December (Fig. 3A) was incomplete since a great many shrimp remained as males for another entire year before undergoing transition during their third spring (at age 2). Given the fact that a few male and transitional shrimp > 15 mm CL were sampled at various times of year, the possibility that a few individuals do not change sex until their fourth year (age 3) could not be ruled out. Even though the transition of younger (age 1) shrimp in the spring was incomplete, a sizable number of non-ovigerous Stage I shrimp which completed transition in their first year were collected in March (Fig. 3J). These new females were considerably larger (by about 2 mm CL) than their male counterparts, suggesting that it was the larger, faster growing, individuals which underwent transition at age 1. Allen (1963) also reported that the largest 0 age-group males changed sex first.

TABLE 7.—Percent total number of male, transitional, and female *Pandalus montagui* collected at all depths and times of year in four areas in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Area 1	Area 2	Area 3	Area 4	Total
Total males	82.3	63.4	67.1	77.9	68.1
Transitionals	1.6	3.0	11.5	12.3	7.1
Females/Stage I	14.0	25.4	16.8	5.5	18.8
Females/Stage II	0.0	2.6	0.4	0.0	1.3
Total non-ovigerous females	14.0	28.0	17.2	5.5	20.0
Ovigerous females	2.2	5.7	4.2	4.3	4.7
Total females	16.1	33.6	21.4	9.8	24.8
Total no. individuals	186	1,037	827	326	2,376

TABLE 8.—Percent total number of male, transitional, and female *Pandalus montagui* collected in all areas and times of year by depth range in Penobscot Bay during 1980-81. (Females are categorized by reproductive stage.)

Sex/Stage	Shallow (12-25 m)	Moderate (25-50 m)	Deep (50-85 m)	Total
Total males	82.4	61.6	75.3	68.7
Transitionals	1.1	5.8	7.1	5.9
Females/Stage I	14.2	24.0	10.9	18.1
Females/Stage II	0.0	2.7	0.1	1.5
Total non-ovigerous females	14.2	26.6	11.1	19.6
Ovigerous females	2.3	5.9	6.6	5.8
Total females	16.5	32.6	17.6	25.4
Total no. individuals	176	1,013	732	1,921

Older shrimp which changed sex in their second year had not yet appeared as females in March (Fig. 3J), suggesting that sex transition in older shrimp was delayed; it may also have been less rapid, particularly since growth was considerably reduced after the first year. Earlier studies of *P. montagui* indicated that sex transition in two locations in the North Sea persisted for most or all of the year. Mistakidis (1957) noted that sex transition occurred from May to December in the Thames estuary whereas Allen (1963) collected transitional individuals throughout the year in Northumberland, but primarily in June. The timing of minimal sex transition in Penobscot Bay and Northumberland was identical (November-December); Allen (1963) reported that this was when males were sexually active. Couture and Trudel (1969b) reported that most sex transition occurred in October at Grand-Rivière; a few transitionals were collected in July and August but none in May and June. Sex transition in the North Sea, as reported by Mistakidis (1957) and Allen (1963), was accelerated in comparison with Penobscot Bay; some individuals changed sex in their first year, but most did so in their second year. Ages at sex transition at Grand-Rivière, on the other hand, were the same as in Penobscot Bay, i.e., some in their second year, most in their third year, and some in their fourth year.

Seasonal Changes in Size (Age) Composition

Two size-groups of male *D. leptocerus* were observed in the Penobscot Bay during the winter (Fig. 2A, E, G) and only one in the summer (Fig. 2K); similarly, female length-frequency distributions in November-December were bimodal (Fig. 2B), but a single size-group was dominant in the summer (Fig. 2L). Presumably, most of the older (age 2) males either die or migrate out of the upper Bay in the

spring since the younger age-group made up the entire population in the summer. Most of the females apparently spawn once and die after their eggs are hatched since very few older females were found in the winter. The presence of a few larger males in October (Fig. 2N) suggested that a few survive into their third fall and mate twice (or three times if they mature during their first year). Further evidence that most female mortality occurs following hatching while male mortality is delayed until later in the spring was indicated by the seasonal changes in relative abundance of males and females (Table 3): females decreased from 50 to 35% of the population between early December and late January while males decreased more slowly from 65% in January to 48% in the summer.

Age-2 *P. montagui* which were either in transition or were still males in March had mostly become females by the summer (although a few transitionals and large males still remained). The single large size-group of first-maturing Stage I females in the summer (Fig. 3M) presumably included age-1 females at a modal length of 13 mm CL and age-2 females at about 15 mm CL. At the same time, there appeared to be at least two size-groups of Stage II females in July-September (Fig. 3N) which had carried eggs the previous winter (Fig. 3C, G). Ovigerous females captured in November-December 1980 (Fig. 3C) presumably included first-time spawners at 12-15 mm CL and one or two groups of repeat spawners at 15-19 mm CL. Excluding the single female at 10 mm, two or three age-groups of ovigerous females were apparent in January (Fig. 3G). As indicated earlier, the relative abundance of the different age-groups in November-December and January showed that repeat spawners may have accounted for a larger percentage of the ovigerous females earlier in the winter.

Growth and Longevity

Male and female *D. leptocerus* which hatched in the winter of 1979-80 reached 6.0-8.5 mm CL by October of their first year (Fig. 2N, P) and grew relatively slowly during their first winter; by March they had reached 7-10 mm CL and the females were slightly larger than the males (Fig. 2G, H). This difference in size-at-age was also discernible in January (Fig. 2E, F). Growth was rapid during the spring of the second year prior to the beginning of the breeding season: males increased about 3 mm in carapace length by the summer while females increased by 4 mm (Fig. 2K, L). The difference in modal lengths between males and females had increased further by October (Fig. 2N, P) as growth increased modal carapace lengths by an additional 0.5-1.0 mm for both sexes. Growth between early October and late November when ovigerous females were first sampled was negligible, if October 1981 data can be compared with November 1980 data. During this same short period of time the relative abundance of the younger, newly recruited, age-group (males and females) increased dramatically. (A reduction in somatic growth can be expected at a time of rapid egg development since female growth ceases once their eggs have "dropped" and they are unable to molt). This species reached a maximum observed size of 19 mm CL (not included in compiled length frequencies), but most individuals did not exceed 16 mm CL. Unless older individuals migrate completely out of Penobscot Bay and were therefore not sampled during this survey, the maximum lifespan of *D. leptocerus* in the Bay appears to be about 2 yr and 9 mo, although the bulk of the population apparently survives for only 2 yr.

The first evidence of newly recruited 0 age-group *P. montagui* was in November-December 1980 (Fig. 3A, B). Individuals which remained as males during their second year grew from about 7-9 mm CL in November-December of their first year to 8-10 mm CL in March (Fig. 3H) and 10-13 mm CL in their second summer (Fig. 3K). As was observed for *D. leptocerus*, the growth rate increased in the spring. Age-1 shrimp which became females during their second spring reached 10-12 mm CL in March (Fig. 3J) and 12-15 mm CL in the summer (Fig. 3M). Comparison of November-December 1980 and January 1981 data (Fig. 3C, G) with summer 1981 data suggested that growth of mature females in the fall was negligible; the same was true for the males. The maximum observed size was 19.5 mm CL; females as large as 17-18 mm CL were collected in the winter (Fig. 3C, G). These results suggested that *P. montagui* in Penobscot Bay normally spend 1-2 yr as males and as many as 3 yr as females. The maximum lifespan is probably 4 yr since shrimp that remain males for 2 yr do not complete sex transition until their third year and function as females in their third and fourth years.

Growth at Grand-Rivière was sufficiently slower that males there were 2-3 mm CL smaller by the end of their first year than they were in Penobscot Bay. This difference in growth could be a result of lower summer bottom temperatures in the Gulf of St. Lawrence. A temperature range of $-1°C$ (in May) to $3°C$ (in October) was reported in 54 m at Grand-Rivière in 1965 (Couture and Trudel 1969a). Temperatures recorded in lower Penobscot Bay during the same months of the year at 40-60 m were

considerably higher, i.e., 3°C west of Islesboro in May 1970[6] and 11°-12°C at various stations in the lower Bay in August 1976[7]. In Penobscot Bay, *P. montagui* were smaller after their first year's growth than in the two North Sea locations (Mistakidis 1957; Allen 1963) but attained approximately the same size by the end of the second year. Males in the Thames estuary measured 10 mm average CL by November of their first year, and in Northumberland (at 40-60 m depth) they averaged 9.5 mm CL by October; transitionals reached 12.5 mm CL by November of their second year in both locations as compared with 11-13.5 mm CL males of the same age in Penobscot Bay (Fig. 3A), while females in Northumberland reached 14.8 mm CL by November of year 2 as compared with 13-15 mm CL at the same age in Penobscot Bay (Fig. 3C). One-year-old females in Northumberland averaged 10.8 mm CL in October.

Allen's (1963) explanation for this difference between male and female lengths-at-age was that shrimp which mature as females in their first year do so 3-4 wk after males of the same age-group; since growth virtually ceases in the fall and winter, the difference in length attained by the females in the first year is maintained into the third year of life. In Penobscot Bay, on the other hand, very few females mature in their first year; however, if males mature in their first year (this was not determined) and stop growing in the fall before the females, Allen's explanation might apply. It seems more likely that sex transition is a function of size, not age, and that the faster growing 0 age-group shrimp complete sex transition in their first year. Another possible explanation for the difference in size of females which change sex in their second and third years is that there may be two distinct periods of larval production and/or survival. Length-frequency data collected at two different periods during the winter (Fig. 3C, G) did suggest that older females may have spawned earlier than younger females. A 5-yr study of *P. borealis* in the Sheepscot River of Maine[8] failed, however, to reveal any consistent bimodality in larval production during February-April even though at least two age-groups of ovigerous females are commonly observed in commercial catch samples[9]. We contend, therefore, that the most plausible explanation for differences in the sizes of shrimp which become females in their second and third years is a difference in growth rates, especially since a similar difference in size was observed between male and female *D. leptocerus* in which sex remains fixed throughout life.

Pandalus montagui which either began life as females or became females early in their first year were smaller than their male counterparts by November-December of their first year (Fig. 3A, B). It therefore seems probable that the smaller Stage I (6.5-8.5 mm CL) females captured in late January (Fig. 3F) did not grow as rapidly as the larger females in the same age-group which apparently completed sex transition in late December and early January or as shrimp which remained as males for the entire year (Fig. 3D). These differences in length-at-age between 0 age-group males and both groups of females were also evident in late March (Fig. 3H, J). The accelerated growth rate of 0 age-group individuals which changed sex during their first year contrasts with the reported faster growth of *P. montagui* in the North Sea and at Grand-Rivière which began life as females (Allen 1963; Couture and Trudel 1969b).

Winter Migration

During November-December 1980, younger male and non-ovigerous female *D. leptocerus* were predominant in shallow water in area 1 (Figs. 4A, 5A) while the older age group predominated in deeper water (Figs. 4B, C, 5B, C). By late January, the older females were no longer being caught, and the older males had disappeared completely from depths < 50 m (Fig. 4D, E), but accounted for about 50% of the males collected in deep water in area 3 (Fig. 4F). There were older males in areas 2 and 3 (moderate and deep water) in March (Fig. 4G, H). These results suggested that older male shrimp migrated down the Bay into deeper water as the winter progressed and as bottom water temperatures dropped from about 8°C in early December to 1°C in late February and early March in the upper Bay.[10] Their disappearance from the catches,

[6]Muirhead, C. R., and J. H. Wartha. 1971. Temperature-salinity observations, Penobscot Bay, Maine, 1970. Oper. Data Rep. NOS DR-13, U.S. Dep. Commer., NOAA, Natl. Ocean Surv., Off. Mar. Surv. Maps, Oceanogr. Div., Descr. Oceanogr. Sect., Rockville, MD.

[7]Central Maine Power Co., unpublished data, courtesy Richard Birge, Environmental Studies Department, CMP, August, ME.

[8]Stickney, A. P. Environmental physiology of northern shrimp, *Pandalus borealis*. Maine Dep. Mar. Resour., West Boothbay Harbor, ME, Annu. Rep. 1981-82, 15 p.

[9]Diodati, P., S. H. Clark, D. McInnes, R. Tichko, and D. Sampson. 1983. Gulf of Maine northern shrimp stock status -1983. Northern Shrimp Technical Committee, November 1983, 9 p.

[10]Birge, R. P. 1982. Surface and bottom water temperatures, upper Penobscot Bay, Maine, March 1975 - December 1981. Central Maine Power Co., Environmental Studies Department, Report SI-82-3, 45 p.

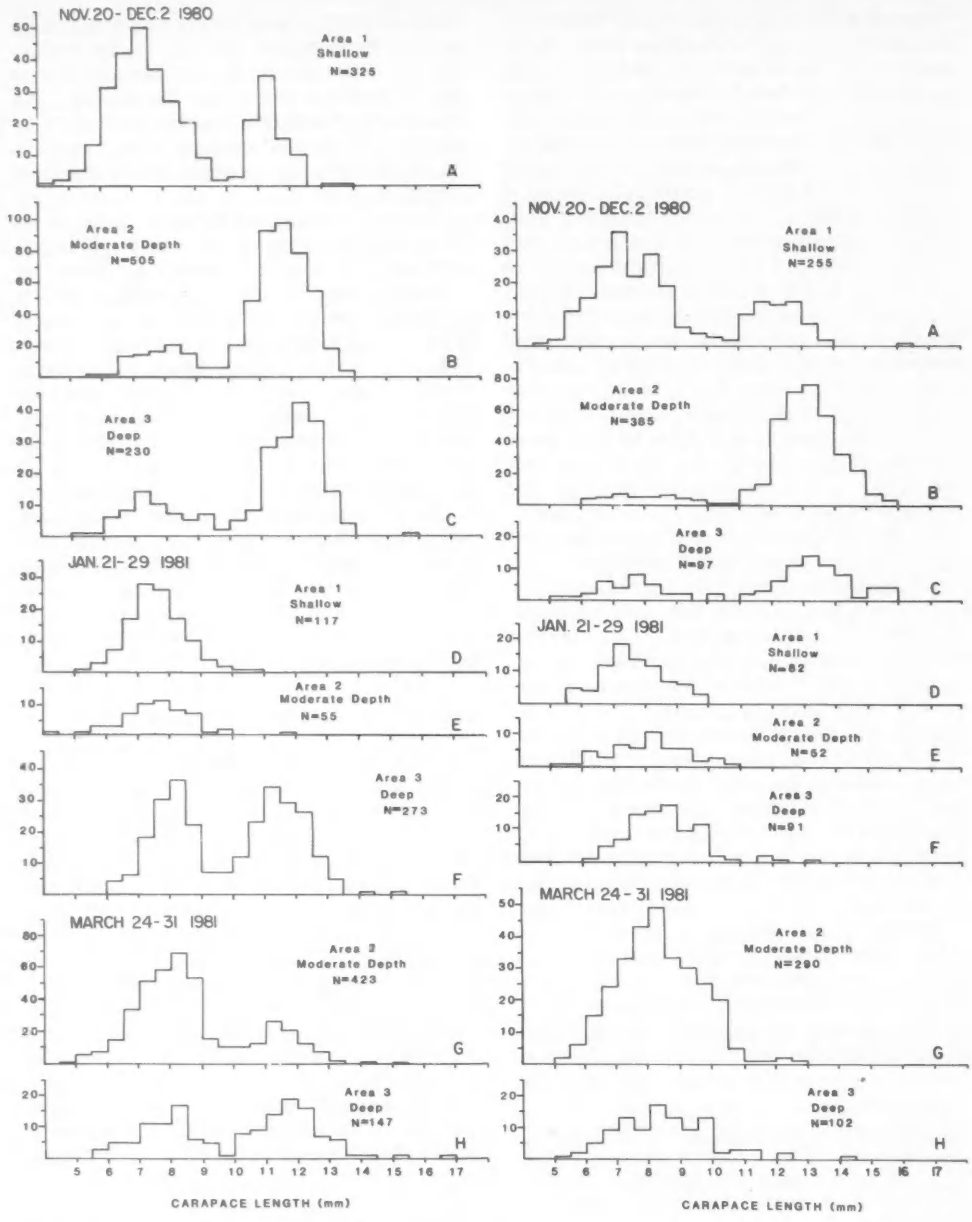


FIGURE 4.—Male *Dichelopandalus leptocerus* numerical length-frequency distributions by area and depth range.

however, may still have been a result of mortality rather than migration. The depth-area length-frequency data also revealed that slightly larger shrimp of both sexes and age-groups were captured in deeper water further down the Bay, suggesting that larger individuals are more likely to migrate than smaller ones.

Older male *P. montagui* also migrated down the Bay into deeper water during the winter: older age-1 males were more abundant than younger 0 age-group males in areas 2 and 3 (moderate and deep water, respectively) in November-December 1980 (Fig. 6A, B, C) and by late January nearly all the older males were in deep water in area 3 (Fig. 6D, E, F), but were not as abundant as the younger males in deep water in area 4 (Fig. 6G). There was no clear evidence that the larger males in either age-group

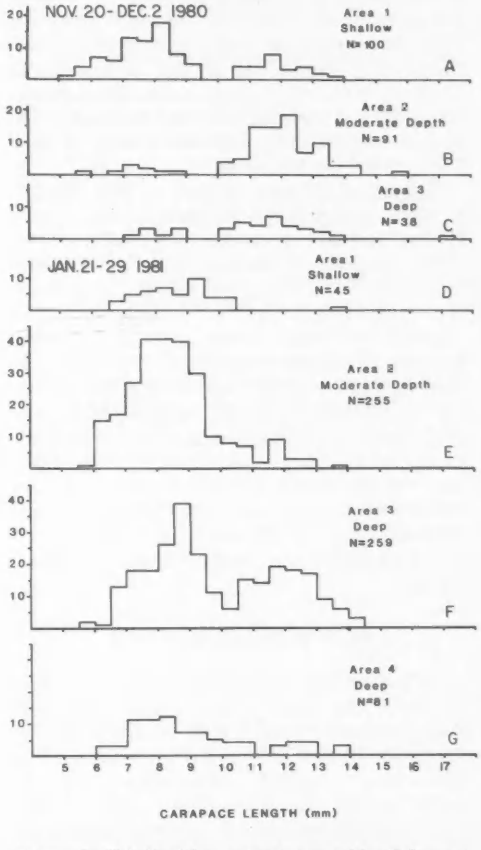


FIGURE 6.—Male *Pandalus montagui* numerical length-frequency distributions by area and depth range.

were more frequent in deeper water and not enough females were collected during any single sampling period to permit an analysis of differential distribution of different age-groups by depth.

Allen (1963) reported an offshore migration of age-1 males to deeper water in the spring and summer in Northumberland waters; Couture and Trudel (1969a) observed the same phenomenon in Grand-Rivière in the summer as the temperature exceeded 6°C and reported that it was triggered by the onset of maturity; earlier maturing males migrated sooner than later maturing males, indicating that migration was a function of size, not age. Mistakidis (1957) and Allen (1963) both reported an offshore migration of *P. montagui* females in the fall; Allen, however, reported that the smaller females stay behind to spawn in shallow water and that there was no "massive" return migration in the spring whereas Mistakidis reported a general offshore fall migration of females and a return migration in the spring. Allen (1963) reported that females in Northumberland which survived to spawn a third time were only found in depths > 100 m.

CONCLUSIONS

This study of the life histories of *Pandalus montagui* and *Dichelopandalus leptocerus* in Penobscot Bay has revealed some notable differences in reproductive characteristics and (apparently) in longevity between the two species. On the other hand, growth rates and migratory behavior were similar.

Most importantly, *P. montagui* is hermaphroditic; *D. leptocerus* is not. In 1980-81, some transitional *P. montagui* were observed during all five sampling periods, but were most common in the early spring; most individuals change sex at the end of their second year but some do so during their first year and a few may not change sex until their third year. Some individuals apparently begin life as females; 15% of the 0 age-group which recruited to trawl catches at 5-10 mm CL in November-December 1980 were females. Ovigerous *P. montagui* were collected over a longer time period, owing, at least in part, to the presence of more age-groups in the spawning population. Most *D. leptocerus* females spawn during their second year, although a few also spawn in their first year; ovigerous females were collected primarily in late November-early December. *Pandalus montagui* spend 1-2 yr as males; individuals which undergo sex transition in their second year may function as females during their second, third, and fourth years while those which change sex in their third year may only function as females for 2 yr. Judging from the

length-frequency data collected during this study, it is unlikely that very many *P. montagui* survive in the Bay beyond age 4. No *D. leptocerus* females older than age 2 were caught in the Bay although some males remained until their third fall (age, 2 yr and 9 mo). Conclusions concerning longevity were complicated by the fact that larger individuals of both species migrated down the Bay into deeper water as the winter progressed and were not captured and by the difficulty of inferring age from length data for the larger size-groups, particularly for *P. montagui*.

Both species were similar with respect to growth and migratory behavior. Growth decreased with increasing age and was seasonal, i.e., rapid in the spring and summer of the first year and the spring of the second year and negligible in the fall and winter. Males of both species reached 7-9 mm CL at age 1 and 11-13 mm CL at age 2. The data suggested that early (age 1) transitional *P. montagui* also grow considerably more rapidly than the remainder of their age group which undergo sex transition at age 2. The slowest observed growth rate was for *P. montagui* which apparently begin life as females and therefore never undergo sex transition. For *D. leptocerus*, females grow more rapidly than males and differential growth is a "fixed" sexual attribute. For *P. montagui*, the fact that the faster growing individuals change sex a year earlier and therefore function as females for an additional year (assuming that fast- and slow-growing shrimp have identical lifespans) means that more rapid growth and early sex transition increase the reproductive potential of the population, as long as enough males remain in the population to mate with the females. Female maturity is clearly a function of size, not age.

The life cycle of *P. montagui* in Penobscot Bay was quite different in several respects from the life cycles of populations which have been studied in the North Sea and at Grand-Rivière, Quebec. *Pandalus montagui* populations in two locations in the North Sea (Mistakidis 1957; Allen 1963) appeared to grow more rapidly in their first year of life than in Penobscot Bay and were composed of a considerably greater proportion of early maturing females, many of which never functioned as males. Growth over the entire lifespan was considerably more rapid in Penobscot Bay and the North Sea than at Grand-Rivière (Couture and Trudel 1969b), but the relative scarcity of females which do not function first as males and the delay of most sex transition until the third year were common to the Canadian and United States populations. In addition to a difference in the timing of maximum sex transition from age 2 (Penobscot Bay and Grand-Rivière) to age 1 (North Sea), the seasonal intensity of sex transition was not the same in three of the populations. Most transitionals were observed in March in Penobscot Bay, in June in Northumberland (Allen 1963), and in October at Grand-Rivière (Couture and Trudel 1969b). Eggs were carried by females in both North Sea locations and in Penobscot Bay during the winter (November-March); at Grand-Rivière most ovigerous females were observed in October.

In Penobscot Bay and the North Sea, sex transition tended to follow the end of the breeding season, whereas in Grand-Rivière, maximum sex transition coincided with the time when most females were carrying eggs (unless sex transition was more common later in the fall when no samples were collected), suggesting that there was a 12-mo interval between the appearance of external female characteristics and spawning at Grand-Rivière, and a 6-9 mo interval in Penobscot Bay and Northumberland. More rapid growth rates in the latter two locations would explain the shorter time intervals between sex transition and spawning. The reproductive cycle in Grand-Rivière was seemingly continuous, beginning in July and ending in June (Couture and Trudel 1969b).

Although an offshore migration of larger male *P. montagui* was observed in Penobscot Bay, Grand-Rivière, and Northumberland, this migration occurred in the winter following the end of the spawning season in the Bay and in spring and summer, prior to spawning, in the other two locations. Similar movements of larger females have been noted in both North Sea populations in the fall. Unlike the other migrations, the one observed in Penobscot Bay was not a spawning migration and may instead have been a response of older shrimp to declining winter temperatures in the shallower waters of the upper Bay. The departure of significant numbers of older shrimp from the Bay could certainly affect any conclusions concerning the size or age structure of either population and their estimated maximum lifespans.

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VISUAL THRESHOLD FOR SCHOOLING IN NORTHERN ANCHOVY *ENGRAULIS MORDAX*

JOHN HUNTER AND RAGAN NICHOLL[1]

ABSTRACT

The visual threshold for schooling was determined for two groups of 50 adult northern anchovy in the laboratory. The index of dispersion and the mean distance to the nearest neighbor were used to measure changes in schooling as a function of light intensity. The threshold light intensity for schooling, 6×10^{-11} W cm^{-2} (2.6×10^{-4} mc), was estimated to occur at a depth of 30 m on a starlit night and at 38 m during a full moon, when the chlorophyll concentration is 0.2 mg Chl a m^{-3}. At 2.0 mg Chl a m^{-3} the threshold occurs at a depth of 8 m on a starlit night and at 20 m under full moon light. Sufficient light appears to exist at night within the upper 10 m for schooling to occur in most of the habitat of the anchovy. The vertical distribution of newly spawned anchovy eggs indicated that the maximum depth of spawning may be similar to the maximum depth of schooling and that the visual threshold for schooling could be used to forecast maximum spawning depth in the sea.

Vision plays a primary role in the maintenance of most fish schools in the sea. Other sense organs, particularly the lateral line, are important in coordinating movements and spacing of fish within the school (Pitcher et al. 1976), but it is unlikely that lateral line sense alone is sufficient for maintaining the integrity of schools at night in the sea. In fact, a large number of laboratory studies indicate that if light is sufficiently reduced, fish no longer maintain schools (Whitney 1969; Blaxter 1970). Thus the visual threshold for schooling and the depth of penetration of light probably determine the maximum depth at which pelagic fishes are able to school at night in the sea.

Our objective was to determine the visual threshold for schooling in adult northern anchovy, *Engraulis mordax*, and to use this information to forecast the maximum schooling depth for anchovy at night in the sea. This calculation is of ecological interest because the maximum depth for schooling is probably also the maximum depth for spawning and for nocturnal feeding. Anchovy spawn only at night and visual recognition of other fish is probably as essential for spawning as it is for schooling. During what we believe was spawning behavior, several males rapidly pursued a female over an irregular path, a tactic probably not possible using senses other than vision. This is a casual laboratory observation and requires further documentation, however. Northern anchovy feed at night as well as in the day (Loukashkin 1970; Hunter and Kimbrell 1980). Light may not be necessary for filter feeding, but it is essential for particulate feeding, although somewhat higher light levels may be required for feeding than for schooling (Hunter 1968). Anchovy migrate toward the surface at sunset (Mais 1974), and schools are less frequently detected at night using sonar and not detected with echo sounders (Smith 1970). Nevertheless, no doubt exists that schooling continues at night because the anchovy fishery is typically a night fishery and because profiles of schools are detectable at night owing to the bioluminescent disturbances their movements produce (Squire 1978).

METHODS

Apparatus and Laboratory Procedures

Two groups of 50 northern anchovy (group 1, mean length = 10.5 cm SL; group 2, = 9.8 cm SL) were maintained in a 4.6 m diameter tank supplied with running seawater (group 1, mean temperature = 16.9°C; group 2, 21.0°C). To simplify photographic analysis the school of 50 fish was constrained to a somewhat two dimensional form by maintaining them in water 45 cm deep. The fish were fed adult *Artemia* at the daily time of 1000, and the tank was cleaned 1 h after feeding.

The tank, which was constructed of blue vinyl, was located in a light tight rectangular enclosure in which the walls and ceiling were covered with white vinyl

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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to diffuse the light. Four light sources were equally spaced around the periphery of the tank; the top of each being just below the tank rim. Each source consisted of a 30 W tungsten microscope lamp with reflector enclosed in a tube. On top of the tube were two color filters; a green acrylic plastic filter (#2414, Rohm and Haas), and a sealed petri dish containing a 5% $CuSO_4$ solution (by weight). To diffuse the light a translucent white acrylic filter (#W-2447, Rohm and Haas) was placed on top of the color filters and light transmitted by the white filter entered a white opal glass globe (13 cm diameter) that formed the top of the source. The lamps were operated for 5 h (10% of lamp life) before they were used to produce test levels of irradiance. These sources were used to produce four test levels of irradiance during a 12-h night. Additionally, four tungsten 100 W household lamps (unfiltered) with reflectors were used for the daytime level of irradiance. These lamps were placed at regular intervals around the perimeter of the tank near the ceiling. Light from these lamps reflected off the ceiling providing a uniformly diffuse illumination. The spectrum produced by the four sources (Table 1) resembles the greenish spectrum typical of anchovy habitat, but the spectrum used in the day was not different from a standard curve for a tungsten lamp and consequently contained an unnaturally high proportion of longer wavelength energy. Our term for the condition when all lamps were off was darkness; under these conditions light was not detectable by a dark adapted human observer and the irradiance was below the sensitivity of a 931A photomultiplier which can detect about 5×10^{-6} mc (meter candle).

To record the effect of light on the schools the fish were photographed from above the tank using a 35 mm automatic camera and flash attachment. The camera was controlled by a timer, and photographs were taken at 30-min intervals for 5 h during the 12-h day, at night in darkness, and at night at the test levels produced by the four sources. Night photographs were taken during a 5-h period commencing 2 h after the end of the 12-h day. Ten photographs were usually analyzed at each light level for each group, but in several tests, 1 or 2 photographs were not analyzed because not all 50 fish could be seen.

Two indices of schooling were calculated for each photograph: an index of dispersion (Pielou 1969), and the mean distance to the nearest neighbor (Hunter 1966). The dispersion index was calculated by superimposing a grid containing 326 quadrats over the projected image of the tank and counting the number of fish occurring in each quadrat. The variance mean ratio ($s^2/\bar{x}$) for the number of fish per quadrat was the index of dispersion. The index was calculated for each photograph, and an average index was computed for each light treatment (n = 8-10 photographs). A dispersion index of 1 indicates a random distribution, whereas higher values indicate aggregation (Pielou 1969) and imply the existence of schooling. Values < 1 imply a uniform distribution over the grid. The mean distance to the nearest neighbor was computed for a random subsample of 10 fish in a photograph. All 50 fish in a photograph were numbered and the subsample of 10 was selected by drawing the fish numbers from a table of random numbers. For each of the 10 fish in the subsample the distance in centimeters to its nearest neighbor was measured (distance between heads), a mean distance calculated for each photograph, and means

TABLE 1.—Spectral functions used to estimate the depth of occurrence of the visual threshold for schooling under the various water types and incident irradiances including spectral irradiance in the laboratory apparatus, moonlight at 3 m below water surface, starlight at the earth's surface (Munz and McFarland 1977), and the relative sensitivity of the dark adapted anchovy eye (*Engraulis encrasicholus*, Protasov 1964).

Wavelengths (nm)		Energy per 25 nm interval (W cm^{-12})			Relative sensitivity anchovy eye
Mean	Interval luminaires	Laboratory luminaires	Moonlight at 3 m depth	Starlight at surface	
400	400-412	3.411×10^{-12}			
425	413-437	1.346×10^{-11}	6.109×10^{-10}	1.978×10^{-11}	0.16
450	438-462	3.402×10^{-11}	6.689×10^{-10}	2.418×10^{-11}	0.53
475	463-487	6.822×10^{-11}	6.820×10^{-10}	2.291×10^{-11}	0.85
500	488-512	9.631×10^{-11}	7.072×10^{-10}	2.374×10^{-11}	1.00
525	513-537	1.069×10^{-10}	7.067×10^{-10}	2.449×10^{-11}	0.75
550	538-562	9.618×10^{-11}	7.283×10^{-10}	5.125×10^{-11}	0.42
575	563-587	5.297×10^{-11}	6.881×10^{-10}	2.838×10^{-11}	0.22
600	588-612	[1]9.494×10^{-12}	5.481×10^{-10}	3.874×10^{-11}	0.08

[1]Wavelength interval = 588-600 nm.

for each light treatment. These measurements are indices of only one characteristic of a fish school, the tendency of individuals to maintain contact with each other and thereby remain in a social group. The polarization of individuals in a school is frequently included in definitions of schooling as the cohesive movements of a school require that fish maintain relatively constant headings and individual distances which gives the polarized appearance of moving schools. This characteristic of fish schools was not measured in our study, thus the visual threshold we estimated was one for the maintenance of schooling in the broadest sense, that is the existence of a group maintained by visual attraction.

Radiometric Procedures, Calibrations, and Computations

Radiometric equipment used in this study consisted of an Optronics spectroradiometer (model 714-V) (calibrated against a radiometric standard) and a photometer (Gamma Model 700). The spectroradiometer was used to measure the spectral irradiance produced by the sources at full lamp output but the treatment levels of irradiance were below the sensitivity of the spectroradiometer. Absolute measurements of light intensity were made 25 cm above the water surface (the difference between this position and within the water would be < 10%). The light treatments were varied by placing neutral density filters in each of the light sources; the neutral density filters were calibrated on an optical bench. Test levels we used were computed from the filter factors for the neutral density filters. The photometer was used to check irradiance levels prior to a test, but we believe the computed values to be more accurate. Irradiance distribution in the tank was mapped using the photometer and the treatment values weighted by tank area so that they represented the average irradiance 25 cm above water surface.

Our laboratory estimates of the visual threshold for schooling were used to calculate the maximum possible depth of schooling in the sea for various levels of incident irradiation and water types. Threshold values in W cm^{-2} were converted to anchovy effective units (W $cm^{-2}{}_{\text{anch. eff.}}$) by weighting the spectrum in the apparatus by the relative sensitivity of the scotopic curve of the anchovy *Engraulis encrasicholus* from an electroretinogram by Protasov (1964) (Table 1). Two levels of night illumination were used, full moon at 3 m depth (2.78×10^{-9} W cm^{-2}), and starlight at the earth's surface (1.08×10^{-10} W cm^{-2}) (both measurements from Munz and McFarland 1977). The depth (meters) in the sea (Z) at which a given threshold (E_z) value occurred was calculated using the equation of Baker and Smith (1982):

$$Z = \frac{\ln\left(\frac{E_z}{E_0}\right)}{-K_t}$$

where E_0 is the incident radiation (full moon or starlight) in anchovy effective units. K_t is the wave length specific attenuation coefficient and is the sum of coefficients for pure water (K_w), dissolved organic matter (K_d), and chlorophyll a (K_c). Tables of coefficients, and equations for calculating these attenuation coefficients, are given by Baker and Smith (1982). In our calculations we assumed that the dissolved organic matter was constant at 0.7 mg l^{-1} which is typical of the anchovy habitat. We calculated K_c for a range of chlorophyll (Chl) a concentrations ranging from 0.1 to 10 mg Chl a m^{-3} and at 25 nm intervals from 425 to 600 nm for each Chl a concentration. Each K_t value for 25 nm increments was weighted by the appropriate anchovy scotopic sensitivity, and the average anchovy weighted $K_{t\ \text{anch. eff.}}$ was used in the final calculation of Z.

Many uncertainties and possible biases exist in such an extrapolation from laboratory to sea conditions: Cloud cover was not considered nor were possible effects of bioluminescence; spectral irradiance values for full moon and starlight of Munz and McFarland (1977) may not be representative of conditions in the anchovy habitat although they are relatively close to those given in photometric units by Brown (1952); variation in dissolved organic matter is not considered; the radiance distribution over 360° in the tank probably does not resemble that in the sea (only downwelling irradiance was considered here); use of the action spectrum based on an electroretinogram of a dark adapted *E. encrasicholus* eye instead of one for schooling of *E. mordax*; and of course, the usual statistical uncertainties. Despite these uncertainties and biases we believe our estimates of schooling depth are the most accurate to date thanks to the models developed by Baker and Smith (1982).

RESULTS AND DISCUSSION

The schooling threshold based on the index of dispersion was between 4.8×10^{-12} and 7.8×10^{-10} W cm^{-2} (Fig. 1; Table 2). At the lower value and in darkness the index of dispersion ($s^2/\bar{x}$ fish per

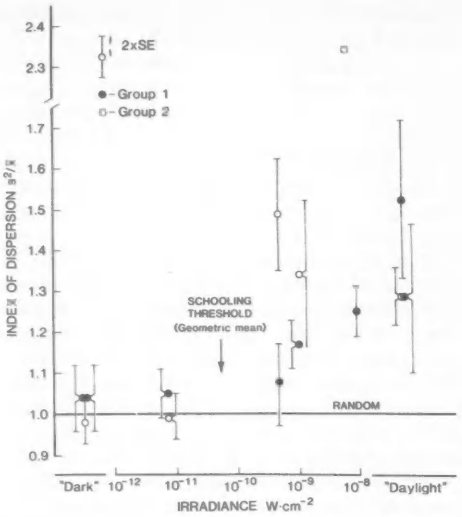

FIGURE 1.—Visual threshold for schooling in northern anchovy. Schooling is indicated by the index of dispersion ($s^2/\bar{x}$). A ratio of 1 implies no schooling as it indicates a random distribution. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. No error bars are given for one value (2.34 ± 0.47) because it falls far beyond the rest of the values. Mean dispersion is shown for four test levels of downwelling irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.496×10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

quadrat) did not differ from unity indicating that the fish were randomly distributed. Hence no schooling existed at the lower irradiance value and in darkness, whereas at the higher value the fish were clearly aggregated. These values delimit a region of about 2 log units of irradiance where one cannot be certain if schooling occurs or not. The actual threshold for schooling must fall somewhere in that region, and we have arbitrarily considered the threshold value to be the geometric mean irradiance of the above two irradiances (6×10^{-11} W cm^{-2}) thereby reducing the uncertainty in the threshold value to about 1 log unit. In subsequent tables and figures we give the upper and lower bounds of the region as well as the threshold value, however.

The variance of the dispersion index, a measure of the variation in school dispersion among photographs, increased sharply at irradiances above the threshold indicating a wide variation in the dispersion of fish among photographs. This can be expected because schooling fish react to fright stimuli, feeding, and many other conditions by altering interfish distances, thereby changing the cohesion or degree of dispersion of the school (Blaxter and Hunter 1982). At light levels below the visual threshold, fish are unable to respond socially to such stimuli, hence the variation among photographs is low.

Mean distance to the nearest neighbor followed the same pattern as we have described for the index of dispersion. Values in darkness and at the lower

TABLE 2.—Mean and standard deviation of the index of dispersion and mean distance to the nearest neighbor for various irradiance levels.

Irradiance (W cm^{-2})	Group	Schooling indices: Dispersion index ($s^2/\bar{x}$) $\bar{x}$	Dispersion index ($s^2/\bar{x}$) s	Mean distance to nearest neighbor (cm) $\bar{x}$	Mean distance to nearest neighbor (cm) s	Number of photographs
1.496×10^{-5} ("daylight")[1]	1	1.28	0.29	17.50	3.71	10
	1	1.52	0.30	12.15	4.10	10
	2	1.28	0.11	24.61	4.94	10
[2]8.92×10^{-9}	1	1.25	0.10	12.19	2.52	10
	2	2.34	0.74	19.49	5.50	10
[2]1.079×10^{-9}	1	1.17	0.09	16.65	3.86	10
	2	1.34	0.27	21.72	7.14	10
[2]4.777×10^{-10}	1	1.07	0.15	18.48	3.86	9
	2	1.49	0.21	18.05	6.62	10
[2]7.785×10^{-12}	1	1.05	0.09	21.87	5.39	8
	2	0.99	0.07	30.40	5.14	10
	1	1.04	0.12	21.20	4.16	9
Dark[3]	1	1.04	0.12	19.61	4.83	9
	2	0.98	0.07	34.12	6.36	10

[1]Unfiltered tungsten lamp.
[2]Filtered lamp - spectrum given in Table 1.
[3]Below sensitivity of 931A photomultiplier.

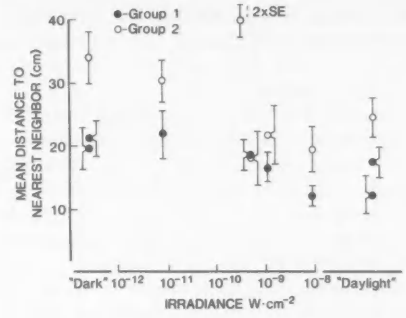

FIGURE 2. – Visual threshold for schooling in northern anchovy is indicated by changes in the mean distance to nearest neighbor. Each point is a mean calculated from 8-10 photographs and bars are ± 2 × standard error of the mean. Mean distance to the nearest neighbor is shown for four test levels of irradiance (log scale), "dark" (below the sensitivity of a 931A photomultiplier), and "daylight" (1.5 × 10^{-5} W cm^{-2}) which was the normal daytime level of irradiance in the apparatus.

irradiance values were not statistically different. Above the threshold the mean distance to nearest neighbor was lower than that in darkness indicating closer spacing among pairs, but no trend with light intensity seemed to exist above the threshold range (Fig. 2). For the purpose of estimating a threshold, however, we believe the index of dispersion is preferable because the criterion for randomness is well defined and the dispersion index takes into account all 50 fish, whereas we used only 10 random pairs per photograph for the nearest neighbor measurements which reduced its precision.

Our calculations indicate that in water of low chlorophyll concentration (0.2 mg Chl a m^{-3}) the threshold irradiance for schooling occurs at a depth of 38 m during a full moon and at a depth of 30 m on a starlit night (Fig. 3). The method of calculation is described in the Methods section on radiometric procedures. Light attenuates rapidly as Chl a concentration increases up to about 2 mg m^{-3} total chlorophyll; at 2.0 mg Chl a m^{-3} the schooling threshold occurs at a depth of only 8 m on a starlit night and at 20 m under full moonlight. Above 2 mg Chl a m^{-3} light attenuates more slowly with increasing Chl a concentration with the threshold at 10 mg Chl a m^{-3} falling at 5 m in starlight and at 12 m in full moonlight. These calculations indicate that sufficient light exists at night for northern anchovy to school within the upper 10 m of nearly all habitats under clear skies, but the maximum possible depth of the schooling would be expected to vary greatly with water type and incident light intensity. An order of magnitude decline in incident irradiation can be expected under the darkest storm clouds (Brown 1952); under these conditions schooling may not be possible at the highest chlorophyll concentrations.

It seems appropriate to use these visual thresholds as estimates of the maximum depth of spawning because spawning probably also depends upon the ability of anchovy to see one another. We calculated the vertical distribution of newly spawned anchovy eggs (0-4 h old, type "S") using data from the unpublished vertical distribution study of Pommeranz and Moser (1983). We selected sets of vertical samples at two stations for which surface Chl a concentrations had been measured and then calculated a mean Chl a concentration for an inshore and offshore series of net hauls. We then estimated the maximum depth for schooling assuming that the surface Chl a was equivalent to an integrated value for the water column as required by the Baker and Smith 1982 model. Spawning occurred closer to the surface at the inshore station which had a high Chl a concentra-

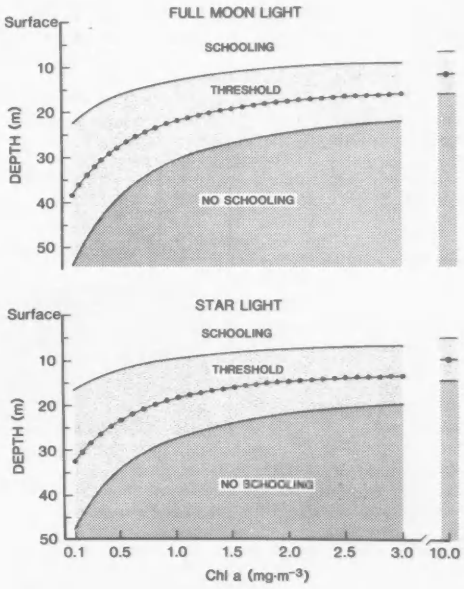

FIGURE 3. – Maximum depth of schooling of northern anchovy in waters of various chlorophyll concentrations (Chl a) under starlight and full moon. Coefficients used in calculations are in Table 1 and in Methods section. Darkly shaded area indicates proportion of water column where no schooling is expected, lightly shaded area indicates depth range of schooling threshold. Central dotted line is the geometric mean.

tion (1.5 mg m^{-3}) than at the offshore station which had a lower concentration (0.24 mg Chl a m^{-3}). At the onshore station only 4% of the eggs occurred below 20 m, whereas at the offshore station 31% were below 20 m. This difference is particularly striking because the inshore samples were taken under a full moon, whereas the moon was in the first quarter when the offshore station was occupied. At both stations the predicted maximum depth for schooling was close to the observed maximum depth for newly spawned eggs (Fig. 4). We may have underestimated the depth of schooling for the offshore (low Chl a) station as we used a starlight value of Munz and McFarland (1977) because no data existed for 1/4 moon. Spawning occurred prior to moonset since spawning occurs between the time of 1800 and 2400 and moonset varied from about the time of 2130 to 0200 (19-25 March 1980). In addition, the offshore station had a deeper mixed layer (about 35 m) than the inshore station (about 10 m) and vertical distribution of anchovy eggs and larvae also may be affected by the depth of the mixed layer (Ahlstrom 1959). Regardless of these uncertainties, these data indicate that underwater visibility may set the maximum depth for spawning of anchovy, although other factors, such as low temperature, might constitute an additional barrier to spawning schools. Thus fish visual thresholds may be a convenient way to establish a general function for estimating the maximum depth of spawning for anchovy and perhaps other pelagic spawning clupeoids in all habitats. Such a general function, that could account for much of the variation in the maximum depth of eggs, could be quite useful in three dimensional models of larval transport or predation. A spawning-depth, water-type function based on visual thresholds seems particularly attractive owing to the considerable cost of accurately measuring the vertical distribution of eggs and larvae even in a single habitat let alone the cost for estimating it for all possible spawning habitats of the population.

To compare the northern anchovy schooling threshold to literature values we converted our radiometric measurements to lux or meter candles (mc), by weighting the spectral irradiance in the apparatus by the human photopic curve, as the literature values are largely in photometric units (see reviews by Whitney 1969 and Blaxter 1970). The visual threshold for anchovy schooling (2.6×10^{-4} mc, Table 3) is about an order of magnitude higher

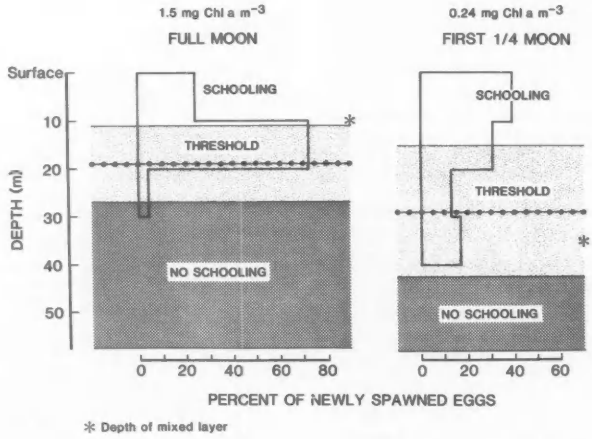

FIGURE 4. – Comparisons of the estimated depths of schooling of northern anchovy and the observed depths of spawning. Estimated depth of schooling calculated from visual threshold estimates (W $cm^{-2}_{anch.\ eff.}$), an assumed dissolved organic matter of 0.7 mg l^{-1}, and the average Chl a concentration and moon phase at the station (1/4 moon phase assumed to be equivalent to starlight) using the model of Baker and Smith (1982). Observed spawning depths at the two stations are indicated by a frequency histogram for newly spawned anchovy eggs where the y axis indicates the depth stratum of the plankton tow and the x axis indicates the percentage of newly spawned eggs taken at each of the 10 m vertically stratified tows. Data are from Pommeranz and Moser (1980) and are for the total number of newly spawned eggs taken over a 4-8 d interval.

TABLE 3.—Upper and lower bound and geometric mean for the visual threshold for schooling of adult northern anchovy, *Engraulis mordax*, in the various energy units.

Energy units	Schooling[1]	No schooling[2]	Geometric mean[3]
Radiometric (W cm^{-2})	4.777×10^{-10}	7.785×10^{-12}	6.051×10^{-11}
Anchovy effective[4] (W $cm^{-2}_{anch.\ eff.}$)	3.079×10^{-10}	5.018×10^{-12}	3.900×10^{-11}
Photometric[5] (mc)	2.048×10^{-3}	3.337×10^{-5}	2.594×10^{-4}

[1]Lowest irradiance level at which schooling occurred.
[2]Highest irradiance level at which anchovy failed to school.
[3]Geometric mean of the irradiance at the upper and lower bounds of the threshold.
[4]Weighted by ERG action spectra for *Engraulis encrasicholus* dark adapted retina (413-612 nm) (Protasov 1964).
[5]Weighted by the 1964 human photopic response (413-600 nm).

than that for jack mackerel (3.5×10^{-5} mc, Hunter 1968), a species associated with anchovy in the California Current. Visual thresholds for schooling in fishes range from about 1×10^{-5} to 1×10^{-1} mc with about 90% (14/16) of the literature values being higher than anchovy (Blaxter 1970). We do not attach much importance to such specific differences because criteria for schooling differ widely and radiometric procedures in the older studies were primitive by today's standard. We suspect the threshold for jack mackerel may have been lower than the northern anchovy because of use of a uniform and highly reflective background in the apparatus and the use of photometric brightness as a unit of measurement. In our work the brightness to the sides and below was much lower than the downwelling irradiation whereas this was not the case in the jack mackerel experiment.

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DISTRIBUTIONAL PATTERNS OF FISHES CAPTURED ABOARD COMMERCIAL PASSENGER FISHING VESSELS ALONG THE NORTHERN CHANNEL ISLANDS, CALIFORNIA

MILTON S. LOVE,[1] WILLIAM WESTPHAL,[1] AND ROBSON A. COLLINS[2]

ABSTRACT

We surveyed fishes taken aboard commercial passenger fishing vessels along the four northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa) within the Southern California Bight. Fourteen species declined in abundance along the Northern Channel Island chain. Colder water forms decreased to the east, while temperate species declined to the west. In the shallowest depth interval (0-36 m), the mean lengths of four rockfish species increased toward the west. In general, the size of these four species also increased with depth. We believe these phenomena are linked to the differences in water temperature between the islands – with cold, California Current water dominant in the west, and warmer Southern California Bight water entrained in the east.

The mainland coast of California is distinguished by two faunal provinces: A warm-temperate Californian Province lies south of Point Conception and a cold-temperate Oregonian Province exists to the north (Seapy and Littler 1980). In shallow waters, the fish fauna of the Californian Province is a mixture of eurythermic temperate and subtropical species, while the Oregonian Province is predominantly a colder temperate region, with few subtropical species present.

Recent studies examining the distributional patterns of marine intertidal invertebrates (Littler 1980; Seapy and Littler 1980), algae (Murray et al. 1980), and seabirds (Hunt et al. 1980) around southern California islands imply there is a replication of these two mainland faunal provinces along the 88 km, east-west lying, northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa) (Fig. 1). Oregonian Province species dominate the western end of the chain, while the fauna of the eastern end is more Californian.

There is little published on the biogeography of fishes around the northern Channel Islands. Ebeling et al. (1980a, b) examined the fish populations of Santa Cruz Island kelp beds, and Hubbs (1967, 1974) stated that the fish communities of San Miguel were closely related to those of central California, while about Santa Cruz fish were typical of southern California. No other work has been published on this topic.

In this paper, we describe one aspect of the northern Channel Islands' fish fauna, utilizing data gathered by the California Department of Fish and Game in their Commercial Passenger Fishing Vessel creel census. This census (fully described in Methods) counted, measured, and noted the location and depth of capture of fishes taken by hook and line on sportfishing passenger vessels in southern California.

Data from this study could not give an unbiased estimate of species composition. Most angling involved fishing with live bait (primarily northern anchovies, *Engraulis mordax*) or with lures simulating fishes, and angling techniques were similar along the island chain. Thus, the sample was biased toward relatively large-mouthed, piscivorous species. However, the purpose of this study was to ascertain distributional patterns of whatever species were taken by these methods, rather than attempting to describe entire fish communities.

METHODS

Fishes taken aboard commercial passenger fishing vessels (CPFV) were sampled by the senior author and by California Department of Fish and Game personnel from April 1975 to December 1978. The sampling units (trips) were chosen randomly, and the population sampled consisted of all regularly scheduled trips by CPFV's operating south of Point Conception to the Mexican border.

The sampler assigned to each boat boarded the

[1]VANTUNA Research Group, Moore Laboratory of Zoology, Occidental College, Los Angeles, CA 90041.
[2]Marine Resources Branch, California Department of Fish and Game, 1301 W. 12th, Long Beach, CA 90813.

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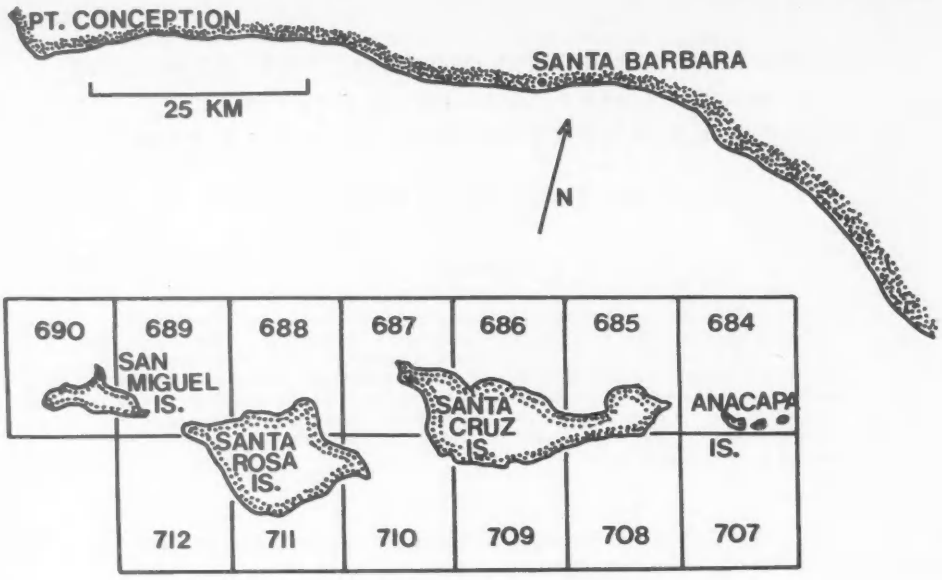

FIGURE 1.—Location and block numbers of sampling sites about the northern Channel Islands, CA.

boat at the beginning of the trip and remained aboard, measuring and identifying all fish caught by the passengers, until the boat returned to dock. A particular effort was made to measure every fish landed, even those returned alive to the water because of undesirability or in compliance with bag or size limit regulations. Also noted were the number of anglers aboard the vessel, the hours of fishing, and the location and depth of fishing effort.

Each fish was placed on a plastic measuring sheet held in a two-sided aluminum frame and the length marked. Total length (tip of snout to tip of depressed caudal fin) was recorded for all fish except members of the jack (Carangidae) and mackerel (Scombridae) families, from which fork length was taken.

A portion of the caudal fin was clipped from each fish measured so that the fish could be recognized later. When fish were brought aboard too rapidly for all to be measured, samplers gave immediate priority to those being returned to the water and measured the remaining fish at the end of fishing or during a break in activity. When samplers were uncertain of the identification of a fish, they retained it for positive identification. After completing a trip, the samplers tallied and recorded by species the data collected. Individual fish lengths were measured on the plastic sheet with a meter stick.

The California Department of Fish and Game has divided marine waters off California into numbered blocks. For this study, we utilized data from block numbers 684-690 and 707-712 (Fig. 1). Care was taken to remove data from mainland fishing sites in block number 684. Block 710 was Santa Rosa Island alone.

We measured fish abundances by catch per unit effort, which was defined as number of fish taken per angler hours (where angler hours = number of anglers × number of hours fished).

RESULTS

One hundred and nineteen trips were made, and the catches from 3,712 anglers were sampled. A total of 23,089 fishes of 78 species were tallied, of which 49 are listed in Table 1. Rockfishes (particularly bocaccio, *Sebastes paucispinis*; blue rockfish, *S. mystinus*; and olive rockfish, *S. serranoides*) and kelp bass, *Paralabrax clathratus*, were numerically dominant. Among the 20 most abundant species, only 4 (*Paralabrax clathratus*; chub mackerel, *Scomber japonicus*; lingcod, *Ophiodon elongatus*; ocean whitefish, *Caulolatilus princeps*) were not rockfishes.

We stratified our data by depth (36 m intervals).

TABLE 1.—Partial list of fishes taken aboard commercial passenger fishing vessels during sampling from April 1975 to December 1978 around the northern Channel Islands. Only those species where 10 or more individuals were taken are listed.

Sebastes paucispinis	3,183
Sebastes mystinus	3,074
Paralabrax clathratus	2,985
Sebastes serranoides	2,632
Sebastes goodei	1,619
Sebastes atrovirens	1.509
Sebastes miniatus	1,119
Sebastes caurinus	1,069
Scomber japonicus	671
Sebastes chlorostichus	632
Sebastes rufus	491
Sebastes carnatus	409
Sebastes entomelas	372
Sebastes constellatus	332
Ophoidon elongatus	304
Sebastes rosaceus	296
Sebastes ovalis	235
Caulolatilus princeps	215
Sebastes levis	197
Sebastes elongatus	195
Sebastes auriculatus	156
Sebastes rosenblatti	148
Semicossyphus pulcher	142
Sebastes rubrivinctus	121
Sebastes eos	120
Sebastes hopkinsi	105
Sebastes chrysomelas	102
Scorpaena guttata	60
Sebastes serriceps	54
Medialuna californiensis	49
Sebastes pinniger	46
Sebastes rastrelliger	43
Genyonemus lineatus	36
Sarda chiliensis	33
Eopsetta jordani	32
Sebastes gilli	21
Sphyraena argentea	20
Citharichthys sordidus	19
Scorpaenichthys marmoratus	19
Trachurus symmetricus	19
Sebastes simulator	18
Chromis punctipinnis	17
Prionace glauca	17
Seriola lalandei	17
Sebastes ensifer	15
Seriphus politus	15
Sebastes nebulosus	12
Paralichthys californicus	10
Sebastes ruberrimus	10

As virtually all fishing effort in waters deeper than 72 m was carried out in the eastern part of the chain, no analyses were conducted of catches in these depths. Most species' abundance trends occurred in the shallowest (0-36 m) depth interval. No samples in 0-36 m were taken in blocks 688, 689, and 709, and none in 37-72 m in blocks 690, 709, 720, 411, and 712.

Fourteen species (Table 2) decreased in abundance along the island chain in 0-36 m (Table 3, Kolmogorov-Smirnov goodness of fit test). Of these, eight species (*Ophiodon elongatus*; *Paralabrax clathratus*; Pacific bonito, *Sarda chiliensis*; *Scomber japonicus*; China rockfish, *Sebastes nebulosus*; yellowtail, *Seriola lalandei*; Pacific barracuda, *Sphyraena argentea*; jack mackerel, *Trachurus symmetricus*) were absent around either the extreme eastern or western end of the chain. The abundance of seven species (*Paralabrax clathratus, Sarda chiliensis, Scomber japonicus, Scorpaena guttata, Seriola lalandei, Sphyraena argentea, Trachurus symmetricus*) decreased toward the west and seven (*Ophiodon elongatus*; copper rockfish, *Sebastes caurinus*; *S. miniatus*; *S. mystinus*; *S. nebulosus*; *S. paucispinis*; *S. serranoides*) decreased toward the east.

The catch per unit effort (CPUE) of six species (*Ophiodon elongatus, Sebastes caurinus, S. miniatus, S. mystinus, S. paucispinis, S. serranoides*) increased in the next (37-72 m) depth interval (Table 4). The largest increases occurred around Anacapa (blocks 684, 707) and the eastern end of Santa Cruz (685, 708). In most instances, catches increased by a factor of 10 or more in these four blocks. The CPUE of three species (*Sebastes miniatus, S. serranoides*, and *S. paucispinis*) were over 100× as great in several blocks.

There was a cline in the mean lengths of four species (*Sebastes caurinus, S. mystinus, S. paucispinis, S. serranoides*) in the shallowest depth interval along the island chain (Fig. 2). All four species were largest in the shallow waters of the more westerly islands, particularly San Miguel.

We compared mean lengths of each species between blocks within the 0-36 m and 37-75 m depth intervals using the Student-Newman-Keuls multiple range test (Sokal and Rohlf 1969). In the shallowest interval, *Sebastes caurinus, S. mystinus*, and *S. serranoides* were largest off San Miguel, while *S. paucispinis* lengths were greatest at San Miguel and Santa Rosa. Two groupings, San Miguel-Santa Rosa and Santa Cruz-Anacapa, were evident in three species (*Sebastes mystinus, S. paucispinis, S. serranoides*) as mean lengths of these tended to form somewhat discrete units. For *Sebastes caurinus*, San Miguel, Santa Rosa, and the west end of Santa Cruz formed one entity – eastern Santa Cruz and Anacapa another.

For these four species, mean lengths were, in most instances, greater in each block in deeper (37-75 m) waters. Though some of the groupings of 0-36 m existed, there was some breakdown of this pattern. In *Sebastes paucispinis*, for instance, the mean lengths of Santa Rosa (block 688) and Anacapa (707) fish were similar, though they were different in 0-36 m.

TABLE 2.—Catch per unit effort × 100, of 14 species taken about the northern Channel Islands in 0-36 m. Block numbers are arranged approximately west to east. The unit of effort is number of fish taken per angler hours (where angler hours = number of anglers × number of hours fished). tr = < 0.01.

Blocks:	690	712	711	710	687	686	685	708	684	707
Ophiodon elongatus	1.1	0.80	0.41	0.23	0.33	0.02	0.03	0.03	tr	0.09
Paralabrax clathratus	0.0	3.62	7.10	0.78	2.65	31.85	2.97	68.33	2.11	22.10
Sarda chiliensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06	0.0
Scomber japonicus	0.02	0.0	0.0	0.97	0.52	0.0	0.21	15.00	0.43	16.88
Scorpaena guttata	0.01	0.0	0.0	0.07	0.0	0.0	0.04	0.03	0.05	1.17
Sebastes caurinus	2.84	7.63	29.68	1.19	1.31	1.45	0.34	0.53	0.16	0.26
Sebastes miniatus	2.92	1.30	0.31	1.26	0.0	0.0	0.04	0.01	tr	0.86
Sebastes mystinus	9.70	17.01	8.85	16.05	3.06	7.61	3.00	1.02	0.21	8.51
Sebastes nebulosus	2.08	2.07	0.36	0.86	0.0	0.0	0.06	0.0	0.03	0.82
Sebastes paucispinis	0.06	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sebastes serranoides	21.31	42.72	16.09	0.69	1.56	3.46	0.41	0.63	0.19	0.86
Seriola lalandei	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.92
Sphyraena argentea	0.0	0.0	0.0	0.0	0.14	0.0	0.0	0.0	tr	tr
Trachurus symmetricus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03	0.0

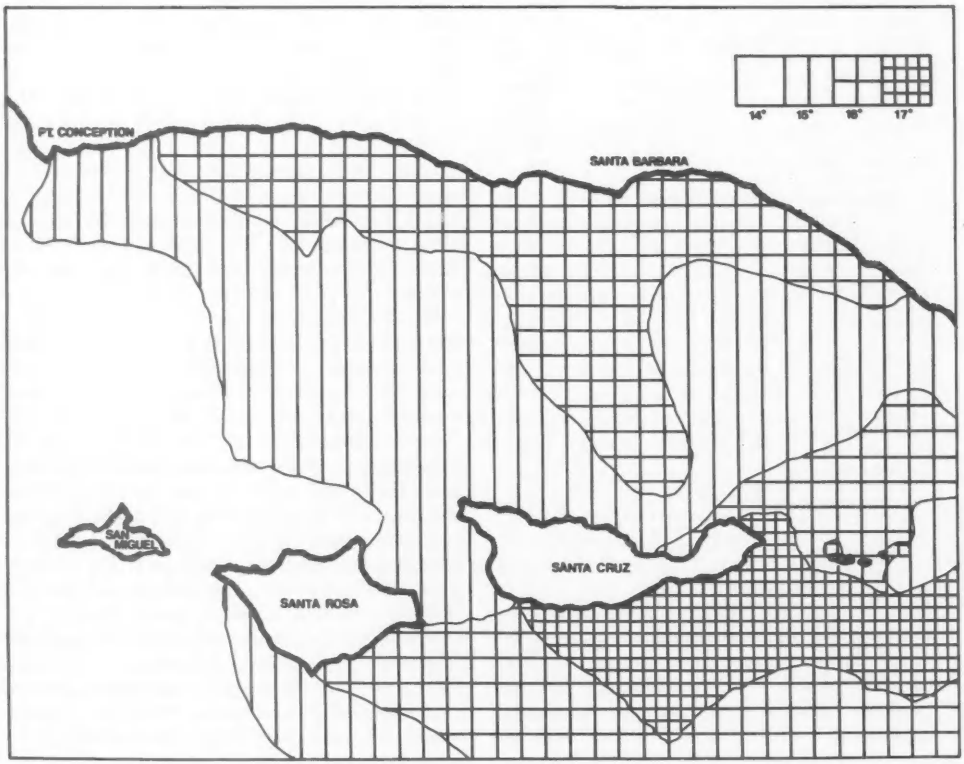

FIGURE 2.—Mean lengths of four species in two depth intervals (0-36 m and 36-76 m) captured along the northern Channel Islands. Dots represent means; bars represent 95% confidence intervals.

TABLE 3.—Fourteen species demonstrating significant catch per unit effort trends (Kolmogorov-Smirnov goodness of fit test) along the northern Channel Islands in 0-36 m.

	Z	P
Ophiodon elongatus	1.64	0.009
Paralabrax clathratus	1.89	0.002
Sarda chiliensis	2.72	< 0.001
Scomber japonicus	1.72	0.002
Scorpaena guttata	2.39	< 0.001
Sebastes caurinus	2.24	< 0.001
Sebastes miniatus	1.57	0.014
Sebastes mystinus	2.10	< 0.001
Sebastes nebulosus	2.69	< 0.001
Sebastes paucispinis	1.49	0.024
Sebastes serranoides	1.97	0.001
Seriola lalandei	2.52	< 0.001
Sphyraena argentea	1.92	0.001
Trachurus symmetricus	2.43	< 0.001

proximity to Point Conception and to the California Current (Reid et al. 1958; Neushul et al. 1967; Kolpack 1971; Seapy and Littler 1980). At Point Conception, as the land extends eastward, the cold California Current continues flowing southward. As it flows offshore, the eastern edge surrounds San Miguel Island and some water spills into the Santa Barbara Channel, flowing along the northern sides of Santa Rosa and Santa Cruz Islands (slowly warming as it travels). Much of the California Current continues to flow southeastward and is later entrained in a slow-moving and warm counterclockwise eddy (Southern California Eddy) within the Southern California Bight. Areas influenced by this eddy, such as Anacapa Island, the southern sides of Santa Rosa and Santa Cruz Islands, and, to a certain extent, the

TABLE 4.—Comparison of catch per unit effort × 100 of six species between two depth intervals (0-36 m and 37-72 m). Block numbers are arranged approximately west to east.

		Blocks										
	Depth	690	688	712	711	710	687	686	685	708	684	707
Ophiodon elongatus	0-36	1.1	—	0.80	0.41	0.23	0.33	0.02	0.03	0.03	tr[1]	0.09
	37-72	—	100.02	—	—	—	1.14	—	0.08	1.53	4.08	0.38
Sebastes caurinus	0-36	2.84	—	7.63	29.68	1.19	1.31	1.45	0.34	0.53	0.16	0.26
	37-72	—	33.28	—	—	—	6.41	—	0.92	8.36	7.68	3.61
Sebastes miniatus	0-36	2.92	—	1.30	0.31	1.26	0.0	0.0	0.04	0.01	tr[1]	0.86
	37-72	—	12.41	—	—	—	6.25	—	0.29	2.04	3.61	0.68
Sebastes mystinus	0-36	9.70	—	17.01	8.85	16.05	3.06	7.61	3.00	1.02	0.21	8.51
	37-72	—	17.08	—	—	—	12.77	—	5.28	16.92	57.21	7.41
Sebastes paucispinis	0-36	2.08	—	2.07	0.36	0.86	0.0	0.0	0.06	0.0	0.03	0.82
	37-72	—	18.21	—	—	—	13.81	—	0.54	10.21	22.81	10.25
Sebastes serranoides	0-36	21.31	—	42.72	16.09	0.69	1.56	3.46	0.41	0.63	0.19	0.86
	37-72	—	4.11	—	—	—	1.63	—	2.89	2.91	22.81	0.28

[1]tr = < 0.01.

Similarly, the distinctions between mean lengths of *S. serranoides* in 0-36 m off Santa Rosa versus Anacapa were not evident in 37-75 m. There was no difference in *S. mystinus* mean lengths between Santa Rosa, Santa Cruz, and Anacapa.

DISCUSSION

Temperature Regime

Previous studies indicate that temperature plays a major role in the community structure of invertebrates and algae along the northern Channel Islands (Littler 1980; Murray et al. 1980; Seapy and Littler 1980), and water temperature was correlated with patterns we observed in fish species abundances and size frequencies. Water temperatures surrounding these islands are strongly influenced by their relative northern sides of Santa Rosa and Santa Cruz, are warmer than areas bathed by the California Current alone. Surface water temperature differences may be as much as 12°C between San Miguel and Anacapa, and 8°C between the west end of Santa Cruz and Anacapa (Hubbs 1967).

Figure 3 exemplifies this condition. It represents the mean of surface temperatures observed by the NOAA-7 satellite on 8 d throughout 1981[3]. Though 1981 was a relatively warmwater year within the Southern California Bight, the influence of the California Current is plain around San Miguel, much of Santa Rosa, and the western end of Santa Cruz Islands. Warm water from southern California bathes southern and eastern Santa Cruz and the

[3]Data taken from observations on 29 January, 15 February, 22 March, 16 May, 4 August, 30 September, 11 October, and 25 November 1982.

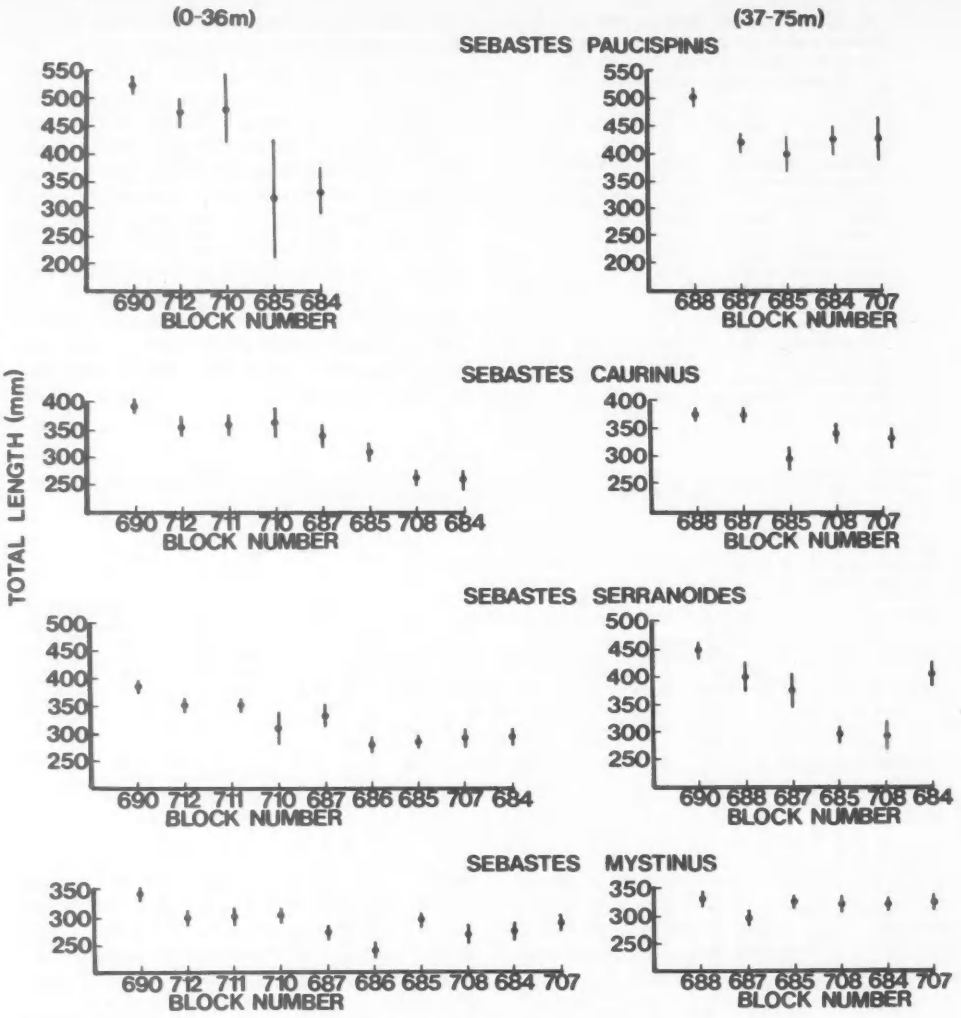

FIGURE 3. – Mean surface temperatures about the northern Channel Islands, based on 8 d throughout 1982 (see text footnote 3).

southeastern corner of Santa Rosa Islands. Warm water occurred close to shore around Anacapa Island, while cooler (perhaps upwelled) conditions occurred slightly offshore to the east.

Fish Distribution

Data from our study suggest that the fish communities of the northern Channel Islands resemble those of the central and southern California mainland. San Miguel and Santa Rosa harbor a more temperate fauna than Santa Cruz and Anacapa. A number of species characteristic of southern California (i.e., *Sarda chiliensis*, *Scomber japonicus*, *Seriola lalandei*, *Sphyraena argentea*) were not found off San Miguel or Santa Rosa, while other southern California species (*Scorpaena guttata* and *Paralabrax clathratus*) were less abundant around

the western islands. Similarly, fishes more characteristic of the Oregonian Province (*Ophiodon elongatus, Sebastes caurinus, S. nebulosus*) were less abundant or absent off Santa Cruz and Anacapa. Evidence from Miller and Lea (1972) bolsters this impression. Nineteen species have geographic range limits along the island chain; of these, 9 (*Anoplarchus purpurescens, Artedius harringtoni, Chirolophis nugator, Hippoglossus stenolepis, Nautichthys oculofasciatus, Radulinus vinculus, Sebastes nebulosus, Stichaeopsis*? sp., *Synchirus gilli*) are temperate and 10 (*Alloclinus holderi, Caranx caballus, Chaenopsis alepidota, Cryptotrema corallinum, Gibbonsia erythra, Gnathephis catalinensis, Gobiesox rhessodon, Leiocottus hirundo, Mobula japonica, Paraclinus integrippinis*) are subtropical or tropical. With only one exception (*Radulinus vinculus*), species on the list typical of the Oregonian Province have their southern limit about San Miguel or Santa Rosa, while most southern forms are limited to Anacapa and Santa Cruz.

Around Anacapa and the eastern end of Santa Cruz, six species (*Ophiodon elongatus, Sebastes caurinus, S. miniatus, S. mystinus, S. paucispinis, S. serranoides*) found in shallow water (0-36 m) to the west were more abundant over deeper (37-72 m) reefs. This is an example of "isothermic submergence" (Briggs 1974). Discussing the mainland southern California fish fauna, Briggs noted that cooler preferring, temperate species sought deeper, cooler waters in the warmer parts of their ranges. All six species are temperate forms, all are found in shallower waters off central California than along the mainland of the Southern California Bight.

The increased length of four rockfishes (*Sebastes caurinus, S. mystinus, S. paucispinis, S. serranoides*) in shallow water around the western islands is at least partially due to a variant of isothermic submergence. Among rockfishes, juveniles are more eurythermic than adults (Miller and Geibel 1973; Love 1978), favoring shallower, warmer waters. Juveniles of these four species were found in shallow waters along all the islands (though in decreasing abundance toward the warmer east), while adults were abundant in shallow waters only in the cooler, more westerly part of the island chain.

Might the trend toward decreased mean sizes in the eastern section be, in part, due to relatively high fishing pressure? There are no records of total fishing effort, stratified by depth, around these islands. However, the California Department of Fish and Game does have data on total angler-hours within each block, derived from operator log-book records. We present these data for 1975-78 in Table 5. It is

TABLE 5.—Partyboat effort about the northern Channel Islands, 1975-78.

	Year	No. anglers	No. anglers-hours
Block 684	1978	11,129	56,571.5
	1977	3,295	14,743.4
	1976	6,152	27,250.5
	1975	7,465	35,296.5
			133,861.9
Block 685	1978	3,048	14,596.0
	1977	2,765	13,951.4
	1976	4,689	23,135.5
	1975	7,088	32,997.9
			84,680.8
Block 686	1978	951	4,588.0
	1977	1,044	5,293.9
	1976	1,500	7,941.0
	1975	2,504	11,803.2
			29,626.1
Block 687	1978	947	4,534.0
	1977	1,213	6,400.0
	1976	2,115	9,928.0
	1975	3,193	16,016.5
			36,878.5
Block 688	1978	1,397	6,723.4
	1977	1,363	6,838.5
	1976	2,745	15,161.5
	1975	2,840	15,425.0
			44,148.4
Block 689	1978	1,259	5,986.4
	1977	1,318	6,423.0
	1976	1,951	9,193.5
	1975	1,692	7,795.5
			29,398.4
Block 690	1978	4,732	19,885.3
	1977	5,065	23,292.7
	1976	6,204	27,576.5
	1975	6,565	28,374.0
			99,128.5
Block 707	1978	3,994	19,580.6
	1977	1,498	7,297.0
	1976	877	3,974.5
	1975	2,448	11,636.5
			42,488.6
Block 708	1978	4,650	23,008.0
	1977	5,931	28,793.8
	1976	2,701	13,807.4
	1975	2,202	10,268.0
			75,877.2
Block 709	1978	1,615	7,796.0
	1977	582	2,975.5
	1976	499	2,208.0
	1975	1,129	6,229.0
			19,208.5
Block 710	1978	5,556	24,435.0
	1977	2,800	13,792.5
	1976	1,019	4,964.4
	1975	2,390	12,544.0
			55,735.9
Block 711	1978	764	3,661.5
	1977	1,264	6,528.0
	1976	556	2,459.0
	1975	739	3,530.0
			16,178.5

our experience that much of the fishing effort in these blocks is in the two depth regimes discussed here. Thus we believe the figures in Table 5 are reflective of the relative fishing effort between blocks.

The data indicate that Anacapa (blocks 684, 707) and eastern Santa Cruz (blocks 685, 708) were indeed among the most heavily fished areas. On the other hand, the westernmost section of San Miguel (block 690), with generally the largest fish size frequencies, was also fished intensively. There are other discrepancies between fishing pressure and size frequencies (Fig. 2). Though block 686 (mid-Santa Cruz) is only moderately fished, *Sebastes serranoides* mean lengths (0-36 m) are similar to those of the more heavily impacted areas to the east. The drop in *S. mystinus* length (0-36 m) begins in block 687 (western Santa Cruz), another moderately fished site. In fact, both *S. mystinus* and *S. caurinus* taken in adjacent block 710 (eastern Santa Rosa) are larger than block 687, even though more fishing took place in block 710. This is not to imply that differences in fishing effort between areas may not play a role. Rather, we believe that the response to temperature by these species is also important.

The marine fauna of the Southern California Bight is notable for its temporal fluctuation. Studies of both fossil (Fitch 1969) and present day records (Hubbs 1948; Radovich 1961; Stephens et al. in press) indicate considerable fluctuation in relative abundance between temperate and tropically derived species. Much of this faunal variability is due to unstable water temperature patterns over the continental shelf. Weakening of the California Current allows for a northerly flow of subtropical water and its associated fauna. During periods of strong California Current, temperate forms increase in abundance. Data for this paper were gathered during the end of a cold cycle (1976) and the beginning of a warm one (which continues to the present–1984).

Juveniles and adults may move with insurgent water masses. This is particularly true of such pelagic or semipelagic species as *Seriola lalandei*, *Sphyraena argentea*, *Sarda chiliensis*, and *Scomber japonicus*. All occur about Santa Cruz and Anacapa Islands (and throughout much of the Southern California Bight) in warmwater periods. During the strong 1983 El Niño, the tropical yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Euthynnus pelamis*, ventured far north of their usual range up to Santa Cruz Island. Even relatively sedentary species may follow currents. The finescale triggerfish, *Balistes polylepis*, was an early migrant into southern California at the beginning of the warm cycle in the mid-1970's and remains relatively common about inshore reefs as far north as Santa Barbara.

Larval transport and subsequent species recruitment may be affected by changes in water masses. During 1983, a number of warm-temperate species (including rock wrasse, *Halichoeres semicinctus*; garibaldi, *Hypsypops rubicunda*; spotted sandbass, *Paralabrax maculatofasciatus*; *Seriola lalandei*; *Sphyraena argentea*; salema, *Xenistius californiensis*) recruited off Santa Barbara, well north of their usual range.[4] Similar unusual northerly recruitment of *Semicossyphus pulcher* and Catalina goby, *Lythrypnus dalli*, occurred during the same period off central California.[5]

Young of-the-year of warm-temperate species have recruited north of their usual range in past warm periods, e.g., 1957-58 (Radovich 1961). In many cases, such as that of the opaleye, *Girella nigricans*, off Monterey, only a single year class (i.e., 1958) survives, leading in succeeding years to populations of similar-sized individuals.[6] During the early 1970's, we observed that the population of *Semicossyphus pulcher* around San Miguel, was composed entirely of large individuals. Perhaps these, too, were the survivors of a successful year class during the 1957-58 warmwater period.

Conversely, during the years of strengthened California Current, species more representative of central California recruit south. The early 1970's were a relatively cool water period and temperate species such as kelp greenling, *Hexagrammos decagrammus*; *Ophiodon elongatus*; *Sebastes mystinus*; and *S. serranoides* young-of-the-year successfully recruited in southern California (Stephens and Zerba 1981; Stephens et al. in press). These maintained themselves in the locally cool habitat at the head of Redondo Submarine Canyon, well after they disappeared from much of the Bight. Water temperature is also responsible for the continuation of long-term temperate species remnant populations on the southern sides of several Baja California points (Hubbs 1960). Here, upwelling water creates suitable conditions for a number of temperate species, which are either missing from, or found in deeper water off of, southern California.

[4]S. Anderson and J. McCullaugh, Marine Science Institute, University of California, Santa Barbara, CA 93106, pers. commun. November 1983.

[5]D. Miller, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. January 1977.

[6]F. Henry, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. November 1983.

It is likely that a continuing warmwater regime has or will alter the species' composition we found. For instance, we might expect less successful year classes among the rockfishes about the eastern islands. Stephens et al. (in press) noted the essentially complete failure of *Sebastes mystinus* and *S. serranoides* recruitment off Palos Verdes and Redondo Beach (on the southern California mainland) during this current warmwater cycle. On the other hand, warmwater species, such as *Paralabrax clathratus* or *Scorpaena guttata*, might recruit more successfully around the previously cool westerly islands. Migratory species, such as *Seriola lalandei*, *Sphyraena argentea*, or *Scomber japonicus* may also be more abundant about these westerly islands.

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MORPHOLOGICAL DEVELOPMENT, IDENTIFICATION, AND BIOLOGY OF LARVAE OF PANDALIDAE, HIPPOLYTIDAE, AND CRANGONIDAE (CRUSTACEA, DECAPODA) OF THE NORTHERN NORTH PACIFIC OCEAN

EVAN B. HAYNES[1]

ABSTRACT

All published descriptions of pandalid, hippolytid, and crangonid larvae of the northern waters of the North Pacific Ocean are summarized. Included are recent changes in nomenclature, definitions of terms used in describing the larvae, and procedures for preparing larvae for examination. The general morphology of larvae of the three families is reviewed, and development of the morphological characters used for their identification is discussed. Principal morphological characters and number of larval stages of known larvae in each family are tabulated. Pandalid larvae are keyed to species and stage of development. A synopsis of the most important morphological characters used for identification is given for larvae of each family, genus, and species. Biology of the larvae is reviewed.

Larvae of the Pandalidae, Hippolytidae, and Crangonidae (order Decapoda, tribe Caridea) are common inhabitants of the neritic meroplankton of the northern (temperate and arctic) waters of the North Pacific Ocean. About 135 species of shrimps are found in these waters, and larvae have been described, at least in part, for 46 species. Many of these descriptions, especially of hippolytids and crangonids, are scattered in various foreign scientific journals.

This report summarizes the morphology of described larvae of the Pandalidae, Hippolytidae, and Crangonidae of the northern North Pacific Ocean and gives instructions for examining them. Development of the characters used for identification is discussed, and a generalized key to stage is given. Larvae of each family, genus, and species are characterized morphologically, and the principal morphological characters and the number of the larval stage are tabulated. Illustrated keys to species and stages are provided for 9 of the 13 pandalid species recorded from the northern North Pacific Ocean. Descriptions of larvae of the remaining four species of pandalids have not been published although their probable morphology has been discussed (Haynes 1980a). References to the published descriptions of larvae of each species and a review of the biology of the larvae are provided.

In the synopses of species, I have selected the most distinguishing larval characters; however, these characters may not always be repeated for similar species, and additional characters may be needed for a specific diagnosis. Other distinguishing characters for the larvae discussed here can often be found in the original published descriptions.

An annotated listing of published descriptions precedes the synopsis of each species. When two or more descriptions are listed, the most complete description is given first. Whenever a "?" appears after a species name or stage in the listings, the author of the original description was uncertain of the identification. In these cases, references to the corrected or verified identification are included in the listing. For a few species, descriptions of larvae are based on specimens from the Atlantic Ocean. It should be noted that morphological characters of larvae of the same species from different geographical areas may vary somewhat (Haynes 1978a).

Taxonomic Nomenclature

I used Rathbun's (1904) nomenclature of Pandalidae except for *Pandalus tridens*. After considering both the larval and adult morphology of *P. tridens* (see Rathbun 1902), I give this species full specific rank (Butler 1980; Haynes 1980a) rather than subspecific rank as *P. montagui tridens*, a Pacific subspecies of *P. montagui* Leach 1814.

Nomenclature of the Hippolytidae follows Holthuis' (1947) revision of the genus *Spirontocaris* sensu lato. Holthuis' revision, based on adult morphology, has been verified from larval morphology (Pike and Williamson 1961; Haynes 1981).

Nomenclature of the Crangonidae is based on the

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821.

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revision by Kuris and Carlton (1977), with one exception. I use only *Crangon*, rather than *Crangon* and *Neocrangon*, because I agree with Butler (1980) and consider Zarenkov's (1965) separation of the genus *Crangon* into two subgenera, *Crangon* s.s. and *Neocrangon*, to be invalid.

The synopsis of characters of *Crangon septemspinosa* larvae also applies to the characters of *C. affinis* larvae. Needler (1941), Kurata (1964b), and Tesmer and Broad (1964) have described these as two species, but according to Makarov (1967), the two species are synonymous. Descriptions of the lar-

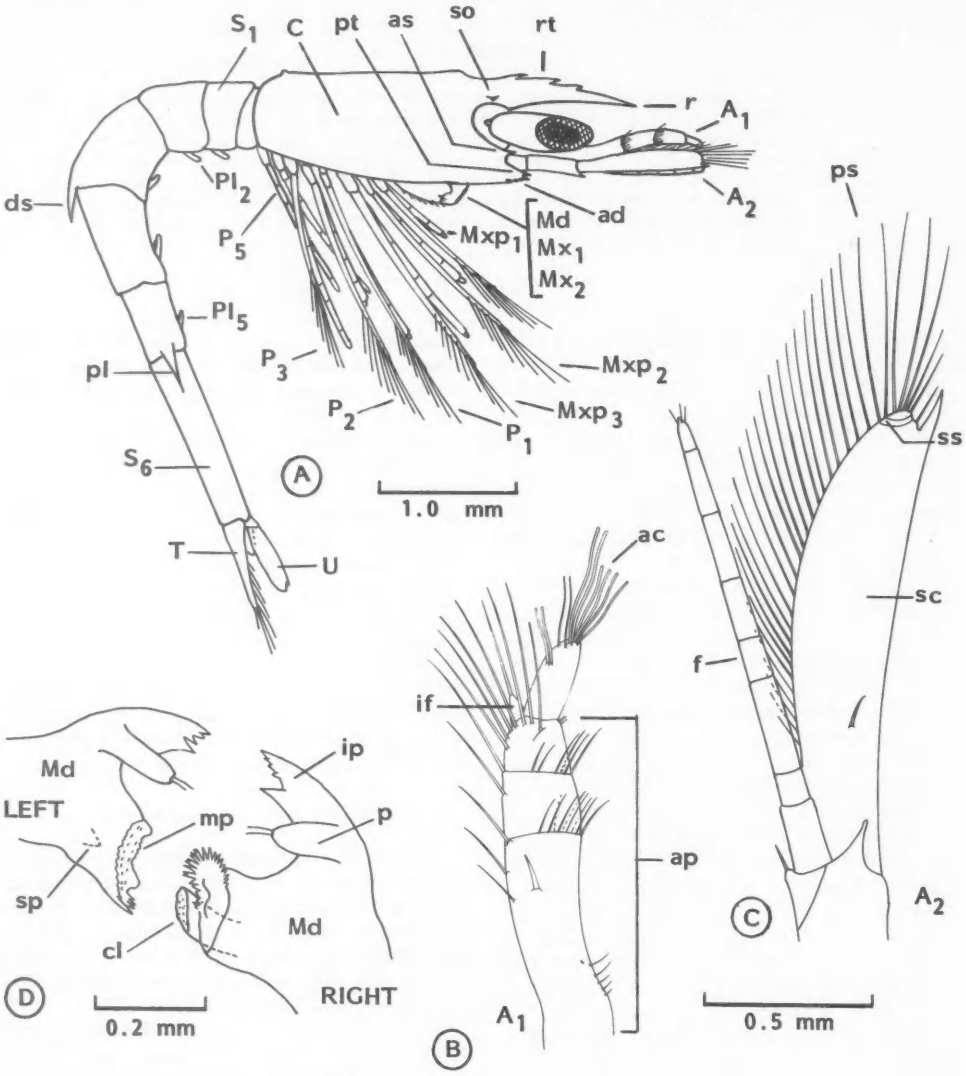

FIGURE 1.—Lateral view and body parts of a diagrammatic decapod shrimp larva. (A) A_1, antennule; A_2, antenna; C, carapace; Md, mandible; Mx_1, maxillule; Mx_2, maxilla; Mxp_1, maxilliped 1; Mxp_2, maxilliped 2; Mxp_3, maxilliped 3; P_1, pereopod 1; P_2, pereopod 2; P_3, pereopod 3; P_5, pereopod 5; Pl_2, pleopod 2; Pl_5, pleopod 5; S_1, somite 1; S_6, somite 6; T, telson; U, uropod; ad, anteroventral denticles; as, antennal spine;

vae of *C. affinis* and *C. septemspinosa* are very similar. More comments on nomenclature for certain species are given in the synopses.

Definition of Terms

I follow Williamson's (1969) terminology for decapod larvae and Haynes' (1979) terminology for larval appendages (Fig. 1). The terms are defined as follows:

abbreviated development – less than five zoeal stages.

carapace length – straight-line distance between the

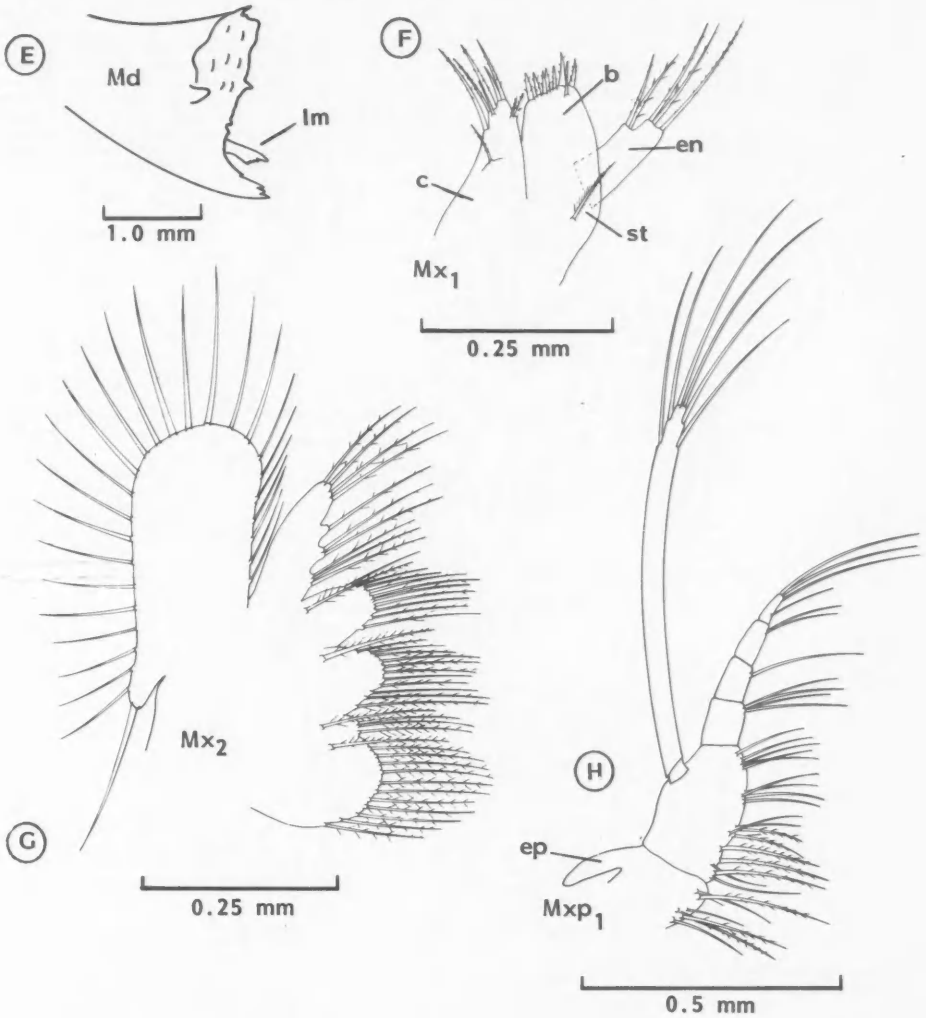

FIGURE 1.–*Continued*–ds, dorsal spine; pl, posterolateral spine; pt, pterygostomian spine; so, supraorbital spine; r, rostrum; rt, rostral teeth. (B) A_1, antennule; ac, aesthetascs; ap, antennule peduncle; if, inner flagellum. (C) A_2, antenna; f, flagellum; ps, plumose setae; sc, scale; ss, scale segments. (D) Md, mandible; cl, curved lip; ip, incisor process; mp, molar process; p, palp; sp, subterminal process. (E) Md, mandible; lm, lacinia mobilis. (F) Mx_1, maxillule; b, basipodite; c, coxopodite; en, endopodite; st, subterminal seta. (G) Mx_2, maxilla. (H) Mxp_1, maxilliped 1; ep, epipodite.

posterior margin of orbit and the middorsal posterior margin of the carapace.

denticles–toothlike projections on anteroventral margin of the carapace.

developed pereopods–segmented pereopods directed vertically under cephalothorax.

juvenile–young form, usually small, sexually immature, and generally resembling adult.

larva–a free-swimming phase in the life cycle of the individual whose morphology (such as body form, appendages, and spination) and habit are different from the adult. The term applies to both zoea and

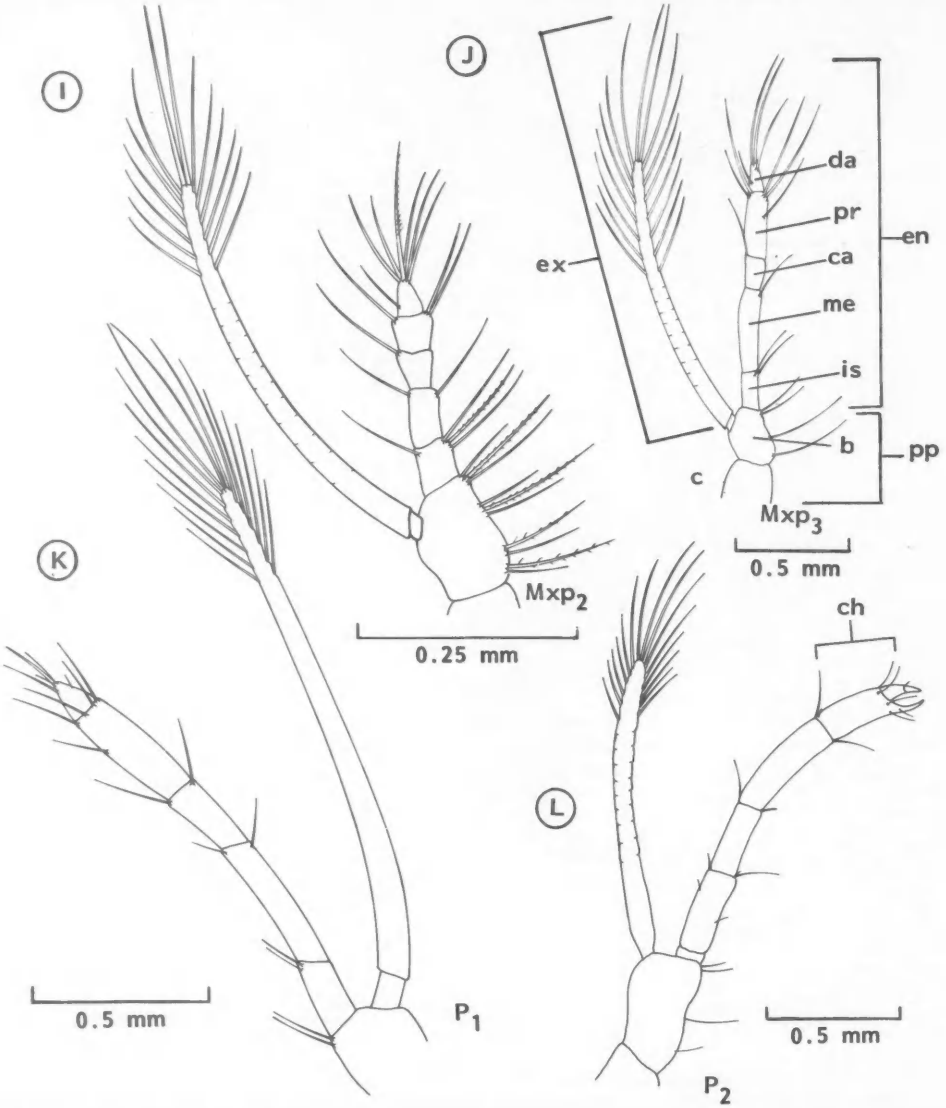

FIGURE 1.–*Continued*–(I) Mxp_2, maxilliped 2. (J) Mxp_3, maxilliped 3; b, basipodite; c, coxopodite; ca, carpopodite; da, dactylopodite; ex, exopodite; en, endopodite, is, ischiopodite; me, meropodite; pp, protopodite; pr, propodite. (K) P_1, pereopod 1. (L) P_2, pereopod 2; ch, chella.

megalopa. (For shrimp, the change from larva to adult is usually somewhat gradual and may include more than one molt.)

megalopa – larva with fully setose natatory pleopods[2] on some or all abdominal somites.

setation formula of telson – setae or spines along the terminal margin of the telson are numbered beginning at the middle of the telson. Thus, 7 + 7 means that the telson has seven pairs of setae along the terminal margin. The first pair is the medial pair.

setose – having setae (bristles).

spine – a sharp, pointed projection, usually long and narrow.

spinose – with many spines.

spiniform – shaped like a spine.

spinule – small spine.

spinulose – with small spines.

stage – intermolt.

subchelate – the dactylopodite (finger) folds against the preceding segment (propodite), as in the first pereopod of crangonid adults.

length – total body length: distance (mm) from the anterior tip of the rostrum to the posterior tip of

[2]In the Decapoda, the development of setose pleopods does not always provide a convenient and clear distinction between zoeal and postzoeal stages. Several species of Pandalidae metamorphose gradually into the postzoeal stage (see Haynes 1976). The term "megalopa", therefore, may include a single stage or several stages depending upon the species. In this paper, the number of larval stages includes all stages before the juvenile stage, regardless of whether the megalopa has one or more stages.

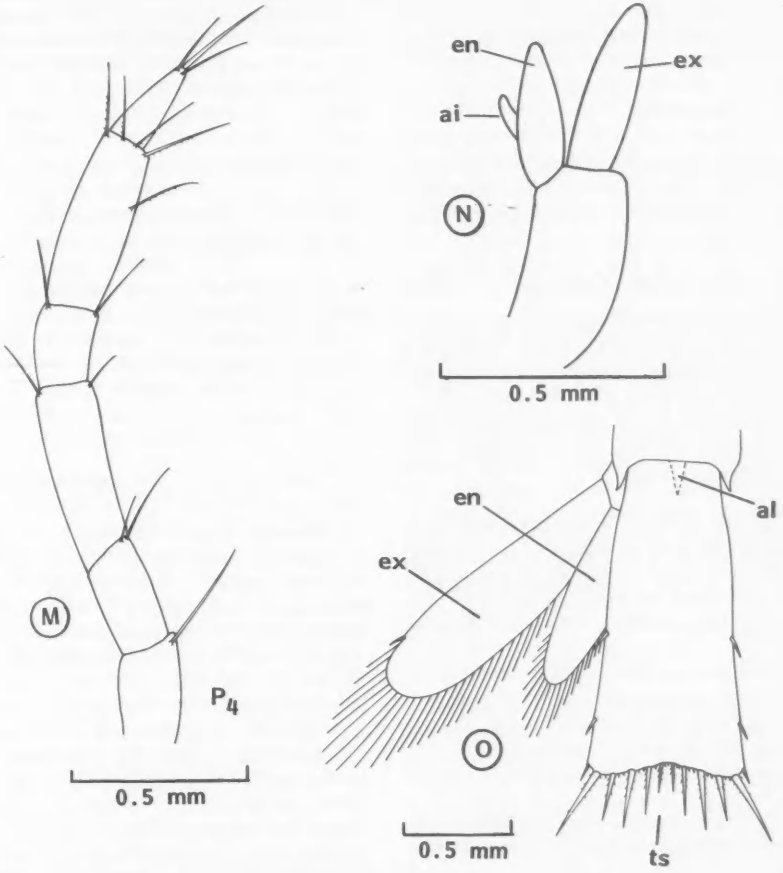

FIGURE 1. – *Continued* – (M) P_4, pereopod 4. (N) Pleopod; ai, appendix interna; en, endopodite; ex, exopodite. (O) Tail fan; al, anal spine; en, endopodite; ex, exopodite; ts, telsonic spines.

telson, excluding telsonic setae or spines.
unabbreviated development – five or more zoeal stages.
undeveloped pereopod – unsegmented pereopod directed anteriorly under cephalothorax.
zoea – larva with natatory setae on maxillipeds, without setose natatory pleopods on some or all abdominal somites 1-5.

Examination Procedure

It is usually necessary to dissect the animal and mount certain appendages on a slide before the identification characters can be used. Visibility of segmentation is often improved by clearing specimens for several days in 10% KOH or full-strength lactic acid. Larvae can be dissected with pins designed for mounting small insects. (The pins are available from most biological supply companies.) After dissecting the larva, place the appendage in a drop of mounting medium (I use Turtox[3] CMC red mounting medium) and cover with a cover glass. Gently press the cover glass to splay hairs and setae and make them easier to examine and count. After mounting the appendages, examine them using a dissecting microscope.

GENERAL MORPHOLOGY OF LARVAE

Pandalid, hippolytid, and crangonid larvae have three major body regions (Fig. 1): head, thorax, and abdomen. The head and thorax are coalesced and are dorsally covered by a common, unjointed cephalothoracic shield, the carapace. The body is divided into 19 true somites which, with their appendages (Fig. 1), are grouped as follows:

1) The head, five indistinguishable fused somites, is covered by the anterior portion of the carapace (C) and has the first five pairs of appendages: antennules (or first antennae) (A_1), antennae (A_2), mandibles (Md), maxillules (Mx_1), and maxillae (Mx_2).
2) The thorax is composed of eight somites that are dorsally fused with, and covered by, the carapace. Each somite has a pair of appendages: Somites 1-3 each have a pair of maxillipeds (Fig. 1A, Mxp_{1-3}); somites 4-8 each have a pair of pereopods (Fig. 1A, P_{1-5}).
3) The abdomen is composed of six somites (Fig. 1A, S_{1-6}) and a terminal segment, the telson (T). The first five somites each have a pair of pleopods (Fig. 1A, Pl_{2-5}). The sixth somite has uropods (U). The uropods, when present with the telson, comprise the tail fan.

CHARACTERS USEFUL FOR IDENTIFICATION OF LARVAE

Understanding the development of morphological characters is necessary for identifying genus, species, and stage of larval development. The following discussion emphasizes the characters most useful for identification. It should be noted, however, that these characters are based on relatively few species of a limited number of genera. For instance, in the family Hippolytidae, the subterminal seta is apparently absent in larvae of *Hippolyte clarki* from British Columbia (Needler 1934) but present in larvae of *H. inermis* and *H. varians* from European waters (Williamson 1957a). The seta may also be present in undescribed *Hippolyte* larvae from the northern North Pacific Ocean. Characterization of the family Pandalidae is based on only two genera, *Pandalopsis* and *Pandalus*. In the northern North Pacific Ocean, described larvae of these two genera develop exopodites only on pereopods 1-2 or 1-3, never on pereopods 1-4. Other genera of the family (e.g., *Plesionika*) may develop exopodites on pereopods 1-4 (Williamson 1957b). Additional descriptions of decapod larvae from the northern North Pacific Ocean will undoubtedly modify the morphological characterizations given here.

Rostrum

In pandalid larvae, the rostrum (Fig. 1A, r) is always long (at least one-third the carapace length). For most species of Pandalidae, the rostrum is styliform in Stage I and does not have teeth (Fig. 1A, rt) until about Stage III. The exceptions are *Pandalopsis coccinata*, *P. dispar*, and *Pandalus platyceros*. In these species, the rostrum is curved in Stage I and has teeth in all larval stages (Berkeley 1930; Kurata 1964a; Price and Chew 1972). In Stage I *Pandalus prensor*, the rostrum curves ventrally between the eyes (Mikulich and Ivanov 1983).

The rostrum of hippolytid larvae may be absent, or, if present, from minute to long. The rostrum is usually without dorsal or ventral teeth in all stages. European specimens of *Eualus gaimardii*, an exception, have two dorsal rostral teeth in the last zoeal stage (Stage V) (Pike and Williamson 1961). If the rostrum is short to long in Stage I, it is also styliform, except in Stage I *Lebbeus groenlandicus* (Fig.

[3]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

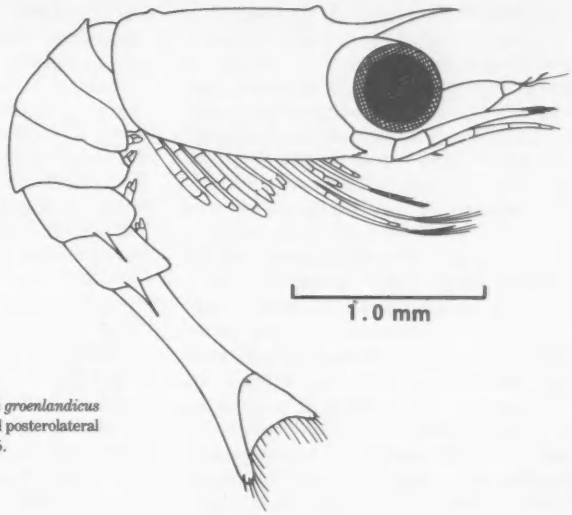

FIGURE 2. – Stage I zoeae of *Lebbeus groenlandicus* showing slightly sinuous rostrum and posterolateral spines on abdominal somites 4 and 5.

2) and *L. polaris*, which have a slightly curved rostrum (Haynes 1978b, 1981). In Stage I *Heptacarpus camtschaticus*, the rostrum is minute and curves slightly downward following the dorsal contour of the eyes (Haynes 1981).

In crangonid larvae, the rostrum is long, spiniform, and without teeth in all larval stages except for Stage I zoeae of *Sclerocrangon zenkevitchi* and *S. boreas*, which lack a rostrum, and Stage I zoeae of *Paracrangon echinata*, which have a spinulose rostrum (Birshteyn[4] and Vinogradov 1953; Kurata 1964b; Makarov 1968).

Spines on the Carapace

The presence or absence of certain spines on the carapace is useful for distinguishing between families and identifying one or more stages. The larval carapace (Fig. 1A, C) may have supraorbital spines (so), pterygostomian spines (pt), antennal spines (as), and anteroventral denticles (ad). Supraorbital spines are absent in all larval stages of the Crangonidae. For pandalid and hippolytid larvae, supraorbital spines are usually absent in Stage I and the megalopa, but present in the intermediate zoeal stages. However, there are some exceptions to these generalizations. Larvae of *Pandalus hypsinotus* have supraorbital spines only in Stages II and III, and larvae of *P. kessleri* have supraorbital spines only in Stage II (Kurata 1955; Haynes 1976). Larvae of *P. prensor* are without supraorbital spines in all larval stages (Mikulich and Ivanov 1983). In the Hippolytidae, *Spirontocaris spinus*, *S. lilljeborgii*, and probably *S. phippsii* have supraorbital spines in all larval stages (the spines are minute in Stage I). *Spirontocaris ochotensis* has minute supraorbital spines in Stage I; whether supraorbital spines develop later is unknown. *Lebbeus groenlandicus*, a species with abbreviated development, has supraorbital spines only in Stage II and the megalopa (Stage III) Pike and Williamson 1961; Haynes 1978b, 1981). In all three families, pterygostomian spines are usually present in all larval stages. Antennal spines are often absent in Stage I but usually develop in later stages. Anteroventral denticles are most prevalent in the early stages and usually, but not always, disappear during larval development. Branchiostegal and hepatic spines are rarely, if ever, present in the larval stages.

Eyes

Development of the eyes is the same for nearly all members of the three families. The eyes are compound and sessile in Stage I and are stalked in later stages. The exception, Stage I *Pandalopsis coccinata*, has compound eyes that are only partially attached to the carapace (Kurata 1964a).

Antennules

In the Pandalidae and nearly all hippolytid and

[4]Translator's spelling of "Birstein".

crangonid larvae, the peduncle of the antennule (Fig. 1B, ap) is unsegmented in Stage I and becomes three segmented later, usually in Stage II. The exceptions are Stage I *Sclerocrangon boreas*, which has a 3-segmented antennule; Stage II *Eualus suckleyi* and *E. fabricii*, which have 2-segmented peduncles; and both Stages I and II *Lebbeus polaris* and *L. groenlandicus*, which have unsegmented peduncles.

In Stage I pandalid and hippolytid larvae, the inner flagellum (Fig. 1B, if) of the antennule is usually a plumose seta, whereas in Stage I crangonid larvae, it is usually a setose spine. The only described exceptions are Stage I larvae of *Pandalus prensor*, *Sclerocrangon boreas*, *S. salebrosa*, and *S. zenkevitchi*. In Stage I *Pandalus prensor*, the inner flagellum is spine shaped and has a few simple setae medially. In Stage I *S. boreas*, *S. salebrosa*, and *S. zenkevitchi*, the inner flagellum is an oblong projection that is naked except for a few minute, simple setae terminally (Birshteyn and Vinogradov 1953; Makarov 1968; Haynes 1978b, 1981; Mikulich and Ivanov 1983).

Antennae

Segmentation of the tip of the antennal scale (Fig. 1C, sc, ss) is an important characteristic for distinguishing crangonid larvae from pandalid and hippolytid larvae. In crangolid larvae, the scale tip is unsegmented in all stages. In pandalid and hippolytid larvae, the scale tip is unsegmented in only four species: *Pandalopsis coccinata*, *Pandalus kessleri*, *P. prensor*, and possibly *Heptacarpus* (= *Spirontocaris*) *tridens* (Needler 1934; Kurata 1955, 1964a, b; Mikulich and Ivanov 1983). The absence of segmentation of the scale tip of *Pandalopsis coccinata*, *Pandalus kessleri*, and *P. prensor* is related to the extremely precocious development of these species. *Heptacarpus tridens*, however, has unabbreviated development (Needler 1934) and, presumably, a segmented tip. Needler (1934) may not have observed segmentation of the scale in *H. tridens* because she based her description on unstained larvae (staining emphasizes segmentation (Haynes 1976)).

Mandibles

Mandibles (Fig. 1D) are described for most pandalid larvae, but descriptions of mandibles for hippolytid and crangonid larvae in the northern North Pacific Ocean are usually limited to Stage I. I have supplemented these limited descriptions with information on larvae from other areas, particularly the North Sea. Descriptions of late stage larvae from the northern North Pacific Ocean are needed, however, to verify development of mandibles in hippolytid and crangonid larvae.

Zoeae of Pandalidae, Hippolytidae, and Crangonidae have similar mandibles in all stages, and both molar and incisor processes are present. In Stage I, the incisor processes of the left and right mandibles are typically biserrate or triserrate. The number of teeth increases in later stages. In some species, the left mandible also has a subterminal tooth and a lacinia mobilis (movable spine adjacent to incisor process; Fig. 1E). The subterminal tooth and lacinia mobilis are usually, if not always, absent on the right mandible. In the Crangonidae, the incisor process eventually becomes a molar process, usually at the megalopa.

The most distinctive character of the mandible is the absence of a palp in the zoeal stages. This palp first appears in the megalopa or first juvenile stage of Pandalidae and in the megalopa or later stages of the Hippolytidae. In one exception, *Pandalopsis coccinata*, the palp is present and segmented as early as Stage I (Kurata 1964a). The palp is absent in all stages of Crangonidae, including the adults.

The mandibular palp of the Hippolytidae may develop somewhat later than the mandibular palp of the Pandalidae. For instance, in some species of Hippolytidae, the palp may not appear until as late as the third or fourth juvenile stage (Lebour 1936), and in some genera, such as *Hippolyte*, the absence of the palp in the adult may mean the palp is absent in the larvae also. The palp eventually becomes three segmented in the Pandalidae and two segmented in the Hippolytidae.

Maxillules

Lebour (1930) stated that *Pandalus* larvae have no subterminal seta (Fig. 1F, st) on the basipodite of the maxillule (Fig. 1F, Mx_1, b). Yet, the seta is present in some or all larval stages of *Pandalus kessleri*, *P. tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, *P. jordani*, *P. hypsinotus*, and *Pandalopsis coccinata*. The seta is also present in the early stages of *Pandalus montagui*, *P. propinquus*, *Pandalina brevirostris*, and *Dichelopandalus bonnieri* that were collected from waters off Great Britain (Needler 1938; Kurata 1955, 1964a; Pike and Williamson 1964; Modin and Cox 1967; Lee 1969; Haynes 1976, 1978a, 1979, 1980a). The subterminal seta is absent in hippolytid and crangonid larvae described from the North Pacific Ocean but is present in larvae of *Hippolyte inermis* and *H. varians* from waters off Great Britain (Lebour 1931). According to Gurney (1942) and Pike

and Williamson (1964), the seta is probably the vestige of an exopodite; however, Williamson (1982) regards it as a vestigial epipodite or pseudoepipodite.

Maxillae

Development of the scaphognathite (exopodite) of the maxilla (Fig. 1G) is related to development of the larvae. Most species that lack precocious development have a scaphognathite that is not lobed proximally and has only a few (usually ≤ 12) plumose setae only on its outer margin. The scaphognathite gradually becomes lobed proximally in subsequent stages, and the outer margin becomes fringed with many plumose setae. In species with precocious development, the scaphognathite is lobed proximally and fringed with many plumose setae in Stage I.

The number of plumose setae is sometimes used for distinguishing Stages I or II of similar species. For instance, Stage I zoeae of *Pandalus borealis* and *P. goniurus* are similar morphologically, and in these species the scaphognathite has 12 and 5 plumose setae, respectively. In later stages, however, the number of plumose setae fringing the scaphognathite becomes too great to be practical for distinguishing zoeae of similar species.

Maxillipeds

The number of natatory setae on the exopodite of each maxilliped (Fig. 1H-J) is helpful for distinguishing Stage I hippolytid and crangonid zoeae from Stage I pandalid zoeae. All Stage I hippolytid and most Stage I crangonid zoeae have 4, 5, 5 natatory setae on the exopodites of maxillipeds 1-3. In the Pandalidae, all Stage I pandalid zoeae, except *Pandalus stenolepis*, have ≥ 8 natatory setae on the exopodites of at least two pairs of maxillipeds. Stage I *P. stenolepis*, however, cannot be differentiated from Stage I hippolytid and crangonid zoeae based only on natatory setae because Stage I *P. stenolepis* also has 4, 5, 5 natatory setae on the exopodite of each maxilliped.

The absence or reduction in numbers or size of natatory setae on the exopodites of maxillipeds is associated with markedly precocious development. This is especially true for *Pandalopsis coccinata*, *Sclerocrangon boreas*, and *S. zenkevitchi*. Each of these species has only one zoeal stage before molting to the megalopa. In *P. coccinata*, the natatory setae are absent from the third maxilliped. In *S. boreas*, the number of natatory setae on maxillipeds 1-3 is 2, 3, 4, respectively; and the setae are reduced in size. *Sclerocrangon zenkevitchi* zoeae do not have natatory setae on the maxillipeds.

Apparently, the absence or reduction in size of natatory setae prevents zoeae from being planktonic. Zoeae of *S. boreas* and *S. zenkevitchi* (collected at sea) cling to the pleopods of the adult (Birshteyn and Vinogradov 1953; Makarov 1968). Zoeae of *P. coccinata* are rarely, if ever, taken in plankton tows (Kurata 1964a).

Pereopods

The presence of exopodites (Fig. 1J, ex) on certain pereopodal pairs is an important morphological character for identifying shrimp larvae. Exopodites are present on pereopods 1, 1 and 2, 1-3, or 1-4, depending on genus or species (Fig. 1K-M).

Species with unabbreviated development usually develop an exopodite on each pereopod. In most species with ≥ 5 zoeal stages, the exopodites are characteristically small, naked, and nonfunctional at Stage I but functional (have natatory setae) at Stage II or III. Development of exopodites on pereopods tends to be suppressed in species with < 5 zoeal stages.

In the Pandalidae, species that have segmented pereopods directed vertically under cephalothorax (i.e., developed pereopods) in Stage I–*Pandalopsis coccinata*, *Pandalopsis dispar*, *Pandalus kessleri*, *Pandalus danae*, *Pandalus hypsinotus*, and *Pandalus prensor*–also have exopodites or vestigial exopodites on pereopods 1 and 2. Species that have unsegmented pereopods directed anteriorly under cephalothorax (i.e., undeveloped pereopods) in Stage I–*Pandalus tridens*, *P. stenolepis*, *P. borealis*, *P. goniurus*, and *P. jordani*–also have exopodites on pereopods 1-3 (the exopodites are undeveloped in Stage I and develop in later stages). An exception is *P. platyceros*, which in Stage I has developed pereopods and exopodites on pereopods 1-3 (Haynes 1980b).

Of the Hippolytidae, only larvae of the genus *Lebbeus* have developed pereopods in Stage I. *Lebbeus polaris* has vestigial exopodites on pereopods 1 and 2 in Stage I and on pereopod 1 in Stage II. *Lebbeus groenlandicus* has vestigial exopodites on pereopods 1 and 2 in Stage I and no exopodites on pereopods in Stages II or III (Haynes 1978b, 1981).

In the Crangonidae, most species with developed pereopods in Stage I (*Argis crassa*, *A. lar*, *A. dentata*, *Sclerocrangon boreas*, and *S. salebrosa*) are either without exopodites or have rudimentary exopodites. An exception is *S. zenkevitchi*, which has an exopodite on pereopod 1 in Stage I (Birshteyn and Vinogradov 1953).

Which pereopods have exopodites can differ for different species of a genus. For example, the genus *Pandalus* includes larvae that have exopodites on pereopods 1 and 2 or 1-3 (Haynes 1980a). The genus *Eualus* includes larvae that have exopodites on pereopods 1-3 or 1-4 (Haynes 1981). Larvae of *Crangon* typically have an exopodite only on pereopod 1; however, larvae of *C. franciscorum angustimana* have exopodites on pereopods 1 and 2 (Haynes 1980b).

Abdomen

The presence or absence of posterolateral spines (Fig. 1A, pl) on the abdomen is often an important character for identifying the families of caridean larvae. Specimens of pandalid larvae from the northern North Pacific Ocean do not have posterolateral spines. Crangonid larvae, however, usually have posterolateral spines on somite 5, except for larvae of *Sclerocrangon boreas* and *S. zenkevitchi* (Birshteyn and Vinogradov 1953; Makarov 1968). Larvae of Hippolytidae also have posterolateral spines. Posterolateral spines are present on somites 4 and 5 in *Lebbeus* larvae and on somite 5 in *Hippolyte* larvae, but are absent in *Heptacarpus* larvae.

The number of abdominal somites with posterolateral spines is not always the same for all species of a genus. For instance, *Spirontocaris* larvae and most *Eualus* larvae have posterolateral spines on somites 4 and 5, or 5. In some species of *Eualus*, the posterolateral spines may be absent.

Most pandalid and hippolytid larvae lack dorsal spines or teeth on the abdomen. The only known exception is *Spirontocaris spinus*, which has a distinct dorsal tooth on the posterior margin of abdominal somite 3 in the megalopa (Stage VI) (Pike and Williamson 1961).[5]

Of the described crangonid larvae of the northern North Pacific Ocean, only *Crangon septemspinosa*, *C. affinis*, *C. alaskensis*, and *C. franciscorum angustimana* have a dorsal spine (Fig. 1A, ds) on somite 3 (Makarov 1967; Loveland 1968; Haynes 1980b). *Paracrangon echinata* has dorsal spines on somites 1-5 (Kurata 1964b).

Some zoeae have spinules on the posterior margins of abdominal somites. These spinules are present in zoeae of *Pandalus platyceros*, *P. tridens*, *P. stenolepis*, *Eualus suckleyi*, *E. fabricii*, *Argis crassa*, *A. dentata*, and *Crangon communis*. The number and size of spinules decrease in later stages.

[5]This spine is present in all subsequent stages (juvenile and adult) and should probably not be regarded as a larval character.

Telson

The shape of the telson is useful in determining the stage of development of caridean larvae. For most Stage I-III pandalid and hippolytid larvae, the posterior margin of the telson is about twice the width of the anterior margin. At about Stage IV, the shape of the telson narrows posteriorly, and from Stage IV on, the posterior margin of the telson is noticeably less than twice the anterior width. Eventually, the telson narrows posteriorly, as in the adult. Although the telson remains triangular in all stages of crangonid larvae, it is somewhat narrower in the megalopa or first juvenile stage than in earlier stages.

For caridean larvae with unabbreviated development, the typical number of telsonic setae (Fig. 1O, ts) is 7 + 7 in Stage I and 8 + 8 in later stages. These numbers of telsonic setae are seldom exceeded in later stages and are often reduced by either loss or transformation of certain pairs (usually pairs of 2 or 3) into small setae or hairs.

A larger number of telsonic spines are more commonly associated with abbreviated development than with unabbreviated development (Gurney 1942; Pike and Williamson 1964), and this is generally true for caridean larvae of the North Pacific Ocean. For example, *Pandalus kessleri*, a species with four larval stages, has 16 + 16 telsonic setae in Stage I, and *Pandalopsis coccinata*, a species with three (or two) larval stages, has 28 + 28 telsonic setae in Stage I (Haynes 1980a). Examples can also be found in the other families of Caridea. In the Crangonidae, *Sabinea septemcarinata* has 16 + 16 telsonic setae in Stage I and three larval stages, whereas *Sclerocrangon salebrosa* has 22 + 22 telsonic setae in Stage I and one larval stage (Williamson 1960; Makarov 1968). In the Hippolytidae, *Lebbeus polaris* has 9 + 9 telsonic setae in Stage I and four larval stages; *L. groenlandicus* has a total of 21 telsonic setae in Stage I and three larval stages (Haynes 1978b, 1981).

All larvae of Hippolytidae except larvae of the genus *Hippolyte* have an anal spine (Fig. 1O, al). For *Hippolyte* larvae, the anal spine is absent in all described stages. When pandalid and crangonid larvae have unabbreviated development, the anal spine usually appears at about Stage II in pandalid larvae and about Stage IV in crangonid larvae.

However, the presence of an anal spine has little value in the identification of pandalid and crangonid larvae with abbreviated development. In pandalid larvae with abbreviated development, the anal spine first appears at different stages in different species.

For example, the spine is present in Stage I *Pandalus kessleri*, but absent in *P. hypsinotus* until Stage III. The stage at which the anal spine first appears in crangonid larvae with abbreviated development has not been reported.

KEY TO STAGE OF DEVELOPMENT

Larvae of most of the species in this report can be keyed to stage based on development of the eyes and tail fan (Key I; Table 1). Key I is mostly applicable to species whose larval development is not markedly abbreviated (i.e., those with ⩾ 5 zoeal stages). In species with unabbreviated development, exopodites on pereopods are characteristically undeveloped in Stage I and usually have natatory setae beginning at Stage II or III. Most of the species excluded from the key (Table 2) have ⩽ 4 zoeal stages, and exopodites on pereopods are either absent in all stages, vestigial in Stages I and II, or have natatory setae as early as Stage I. Key I is limited because it does not differentiate between the latest stages and uses only one or two characters, which may be absent in damaged specimens.

For pandalid shrimp, Key I can be supplemented by keys to stages for each species (i.e., Keys IV and VI-XI, which have characters not given in Key I and distinguish between the latest stages). With a few

TABLE 1.—Species included in keys.

Pandalidae Haworth 1825	Hippolytidae Bate 1888	Crangonidae White 1947
Pandalopsis Bate 1888	*Eualus* Thallwitz 1892	*Argis* Krøyer 1842
P. coccinata Urita 1941	*E. barbatus* (Rathbun 1899)	*A. crassa* (Rathbun 1899)
P. dispar Rathbun 1902	*E. fabricii* (Krøyer 1841)	*A. dentata* (Rathbun 1902)
Pandalus Leach 1814	*E. gaimardii* (H. Milne Edwards 1837)	*A. lar* (Owen 1839)
P. borealis Krøyer 1838	*E. herdmani* (Walker 1898)	*Crangon* Fabricius 1798
P. danae Stimpson 1857	*E. macilentus* (Krøyer 1841)	*C. affinis* de Haan 1849
P. goniurus Stimpson 1860	*E. pusiolus* (Krøyer 1841)	*C. alaskensis* Lockington 1877
P. hypsinotus Brandt 1851	*E. suckleyi* (Stimpson 1864)	*C. communis* Rathbun 1899
P. jordani Rathbun 1902	*Heptacarpus* Holmes 1900	*C. dalli* Rathbun 1902
P. kessleri Czerniavski 1878	*H. brevirostris* (Dana 1852)	*C. franciscorum angustimana* Rathbun 1902
P. platyceros Brandt 1851	*H. camtschaticus* (Stimpson 1860)	*C. septemspinosa* Say 1818
P. prensor Stimpson 1860	*H. paludicola* (Holmes 1900)	*Mesocrangon* Zarenkov 1965
P. stenolepis Rathbun 1902	*H. tridens* (Rathbun 1902)	*M. intermedia* (Stimpson 1860)
P. tridens Rathbun 1902	*Hippolyte* Leach 1815	*Paracrangon* Dana 1852
	H. clarki Chace 1951	*P. echinata* Dana 1852
	Lebbeus White 1847	*Sabinea* J. C. Ross 1835
	L. groenlandicus (Fabricius 1775)	*S. septemcarinata* (Sabine 1824)
	L. polaris (Sabine 1821)	*Sclerocrangon* G. O. Sars 1883
	Spirontocaris Bate 1888	*S. boreas* (Phipps 1774)
	S. arcuata Rathbun 1902	*S. salebrosa* (Owen 1839)
	S. lilljeborgii (Danielssen 1859)	*S. zenkevitchi* Birstein and Vinogradov 1953
	S. murdochi Rathbun 1902	
	S. ochotensis (Brandt 1851)	
	S. phippsii (Krøyer 1841)	
	S. spinus (Sowerby 1805)	
	S. spinus var. *intermedia* Makarov 1941	

TABLE 2.—Species that cannot be keyed to stage of development using Key I.

Pandalidae	Hippolytidae	Crangonidae
Pandalopsis	*Lebbeus*	*Argis*
P. coccinata	*L. groenlandicus*	*A. crassa*
P. dispar	*L. polaris*	*A. dentata*
Pandalus		*A. lar*
P. danae (Stage III)		*Sclerocrangon*
P. hypsinotus (Stage III)		*S. boreas*
P. kessleri		*S. salebrosa*
P. platyceros		*S. zenkevitchi*
P. prensor		*Sabinea*
P. stenolepis (Stage III)		*S. septemcarinata*

exceptions, Key I can be used to identify larval stages of *Pandalus hypsinotus*, *P. danae*, and *P. stenolepis*. The exceptions are in Stage III *P. hypsinotus*, the endopodite of the uropods is setose and nearly the same length as the exopodite, and in Stage III *P. danae* and *P. stenolepis*, the endopodite is setose and somewhat shorter than the exopodite.

Key I.—Generalized key to stages of most species of pandalid, hippolytid, and crangonid larvae described from waters of the northern North Pacific Ocean. (This key cannot be used for all species, see Table 2 for exceptions.)

1. Uropods absent 2
   Uropods present 3

2. Eyes sessile; telson with 7 + 7 setae . . . . Stage I
   Eyes stalked; telson with 8 + 8 setae . . Stage II

3. Posterior width of telson about twice its anterior width. Endopodite of uropod (Fig. 1O, en) with relatively few setae and noticeably shorter than exopodite (Fig. 1O, ex) . . . . . Stage III
   Posterior width of telson noticeably less than twice its anterior width. Endopodite of uropod setose and about as long as exopodite . . . . . Stage IV and later

LARVAL CHARACTERS OF FAMILIES

Crangonid larvae are relatively easy to distinguish from pandalid or hippolytid larvae; however, pandalid and hippolytid larvae often are difficult to distinguish from each other, especially in the early stages. Briefly, the characteristics of crangonid larvae are 1) the tip of the antennal scale is always unsegmented, 2) the inner flagellum of the antennule is a setose spine or oblong projection, 3) an exopodite is usually only on pereopod 1 and never on pereopods 3-5, and 4) in later stages, pereopod 1 is subchelate, and the telson widens posteriorly. No known pandalid or hippolytid larvae possess this combination of characters.

The following set of characters, although not without exceptions, is probably the most useful set for distinguishing between pandalid and hippolytid larvae of the northern North Pacific Ocean. Pandalid larvae 1) always have a long rostrum (greater than 1/4 carapace length) that has teeth from Stage III on, 2) the basipodite of the maxillule has a subterminal seta, 3) exopodites are only on pereopods 1-2 or 1-3, 4) the abdomen lacks posterolateral spines, and 5) an anal spine is absent in Stage I. On the other hand, hippolytid larvae 1) have a rostrum that is long and without teeth (especially from Stage III on), 2) in all stages, the basipodite of the maxillule lacks a subterminal seta, 3) exopodites are on pereopods 1-2, 1-3, or 1-4 (rather than only on pereopods 1-2 or 1-3), 4) the abdomen has posterolateral spines, and 5) an anal spine is present in Stage I (except larvae of the genus *Hippolyte*).

Late-stage (Stage IV and later) pandalid and hippolytid larvae can often be distinguished from each other by shape of eyes and distance between bases of antennules. The eyes of pandalid larvae taper toward the base, and the distance between bases of antennules is more than the width of an antennule. The eyes of hippolytid larvae are almost cylindrical, and the distance between antennules is less than the width of an antennule. In Stages I-III, distinctions in the shape of eyes and distance between bases of antennules are usually not useful.

Shape of the larva is often helpful in distinguishing between pandalid and hippolytid larvae during the initial sorting. Pandalid larvae, when viewed laterally, have nearly straight antennules, whereas the antennules of many hippolytid larvae curve upward. The abdomen of pandalid larvae appears slightly longer than the abdomen of hippolytid larvae in relation to length of the larva as a whole. These two characters are difficult to quantify and are best learned through examination of specimens of known identity. Additional morphological characters that distinguish larvae of the Pandalidae, Hippolytidae, and Crangonidae are given in the synopsis of each family.

PANDALIDAE

(Genera *Pandalopsis* and *Pandalus*)

In all stages, rostrum long, styliform, or slightly sinuate; plumose seta on inner flagellum of antennule (Fig. 1B, A_1, if); maxillule with or without subterminal seta (Fig. 1F, Mx_1, st) on basipodite; abdomen without dorsal spines, keels, or posterolateral spines; pereopod 1 never subchelate. In Stage I, supraorbital spine absent; rostrum with teeth in some species; anal spine absent in some species. In early stages of most species, antennal scale segmented at tip. In Stages I and II of some species with abbreviated development, vestigial exopodites on pereopods 1 and 2 or 1-3. In later stages, developed exopodites on pereopods 1 and 2 or 1-3, never on 1-4; setose setae on endopodite of each pleopod (Stage V

TABLE 3.—Principal morphological characteristics and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean. + = yes; – = no.

Species	Pereopods bearing an exopodite	Pereopods poorly developed in Stage I	Spinules on abdominal somites	Denticles on carapace margin	No. of telson spines in Stage I	No. of larval stages
Pandalopsis coccinata	1-2	—	—	—	28 + 28	3
P. dispar	1-2	—	—	—	12 + 12	7
Pandalus kessleri	1-2	—	—	—	16 + 16	4
P. danae	1-2	—	—	—	7 + 7	6
P. hypsinotus	1-2	—	—	—	7 + 7	7
P. platyceros	1-3	—	+	+	8 + 8	5
P. prensor	1-2	—	—	—	9 + 9	5
P. tridens	1-3	+	+	+	7 + 7	8
P. stenolepis	1-3	+	+	+	7 + 7	6
P. borealis	1-3	+	—	—	7 + 7	6
P. goniurus	1-3	+	—	—	7 + 7	6
P. jordani	1-3	+	—	—	7 + 7	13

on); telson does not widen posteriorly, has > 1 pair of lateral spines (Stage IV on).

The principal morphological characters and number of larval stages of known larvae of pandalid shrimp of the northern North Pacific Ocean are summarized (Table 3, modified from Haynes 1980b).

Genus *Pandalopsis* Bate

Larval development abbreviated; larvae relatively large (≥ 10.0 mm in Stage I). In all described stages, rostrum with teeth; carapace without denticles; antennal flagellum as long as or longer than body; thoracic appendages noticeably long and thin; abdominal somites without spines or spinules, somites not flared laterally. In Stage I, pereopods segmented; telson with at least 12 + 12 setae; telson jointed with abdominal somite 6.

Pandalopsis coccinata Urita

Only Stage I described, known parentage; figure 7 in Kurata (1964a).

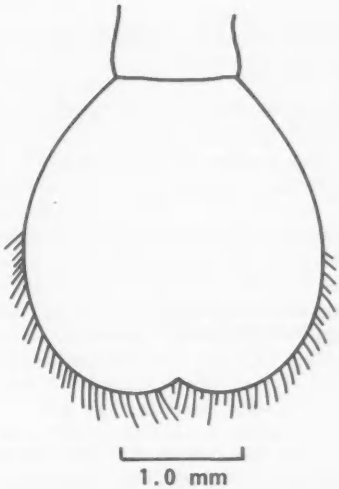

FIGURE 3.—Telson, Stage I zoea of *Pandalopsis coccinata*.

Eyes partially fused with carapace; antennal flagellum same length as body; mandibular palp with 3 segments; seta on basipodite of maxillule; rudimental exopodite on maxilliped 3 and pereopods 1 and 2; telson discoid with 55 or 56 setae (Fig. 3). Length: Stage I, 15.5 mm. Range: Japan (Kurata 1964a), no depth given.

Pandalopsis dispar Rathbun

Possibly 7 larval stages.

Stage I, known parentage; Stages II, III, and V?, from plankton; figures 11-13 in Berkeley (1930).

In all stages, basipodite of maxillule without subterminal seta. In Stage I, eyes sessile; antennal flagellum about 1/4 longer than body. Telson fan shaped in early stages. Until at least Stage V, mandibles without palps; developed exopodites on maxilliped 3 and pereopods 1-2. Length: Stage I, 10.0 mm. Range: Pribilof Islands, Bering Sea to Manhattan Beach, OR; depth, 46-649 m (Butler 1980).

Key II.—Larval stages of *Pandalopsis dispar*.

1. Rostrum curves dorsally (Fig. 4); exopodites on pereopods without natatory setae . . . Stage I

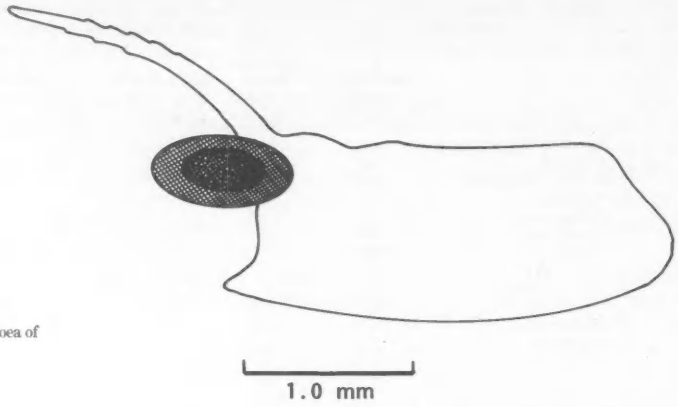

FIGURE 4.—Carapace, Stage I zoea of *Pandalopsis dispar*.

Rostrum horizontal; exopodites on pereopods with natatory setae 2

2. Uropods absent; length of larvae ≤ 13.0 mm . . . . . Stage II
Uropods present; length of larvae > 13.0 mm 3

3. Endopodite of uropod noticeably shorter than exopodite; length of larvae ≅ 16.0 mm . . . . . Stage III
Endopodite and exopodite of uropod same length; length of larvae > 16.0 mm . . . . . Stage IV and later[6]

Genus *Pandalus* Leach

Most species with unabbreviated development. In all stages, thoracic appendages not especially long or thin. In Stage I, larvae usually 5-6 mm long; rostrum usually without teeth; pereopods usually undeveloped and tucked under cephalothorax; telson with 7 + 7 setae; telson not jointed with abdominal somite 6. In early stages of some species, anteroventral margin of carapace with denticles; posterior margin of abdominal somites with spinules.

Pandalus borealis Krøyer[7]

Six larval stages.

Stages I-V, VI (megalopa), and VII and VIII (juveniles); all stages from both known parentage and plankton; figures 1-7 in Haynes (1979).

Stage I, known parentage; Stages II-VII from plankton; figures 1-3 in Kurata (1964a).

Stage I, known parentage; Stages II-VI from plankton; figures 7 and 8 in Berkeley (1930).

Stages I-V from plankton; described as "*P. propinquus* (?)" by Stephensen (1912); figures 22-31 in Stephensen (1912).

Stage III from plankton; described as "*Spirontocaris* larva Nr. 4" by Stephensen (1916); figure 11 in Stephensen (1916). Also described as *P. propinquus*, Stage VI? by Stephensen (1916); figure 17 (chelae only) in Stephensen (1916).

Stage IV from plankton; described as "*Dymas typus*" (?) by Krøyer (1861, as cited in Stephensen 1935). No figures.

"Post larval" from plankton; Plate VII in Sars (1900). Probably megalopa of *P. borealis* (see Haynes 1979).

Not Stages I-VIII *P. borealis* as described by Sars (1900) and figured in Plates I-VI. Correct identity, *Caridion gordoni* (see Berkeley 1930; Lebour 1930).

In all described stages, carapace and abdominal somites not flared laterally; basipodite of maxillule

[6]A later larval stage, probably Stage V or VI, characterized by rostrum with 25 dorsal spines: 1 spine near tip, 14 dorsal spines, 10 ventral spines. Chela of pereopod 2 (Fig. 1, P_2, ch) developed, and carpopodite (Fig. 1, ca) with a few faint segments; abdominal somites and pleopods essentially adult; telson narrows posteriorly and has 7 + 7 slightly plumose, terminal setae and 6 pairs of single lateral spines. Length: 30.0 mm (Berkeley 1930).

[7]Larvae of *Pandalus borealis* and *Pandalus goniurus* are often found together in plankton. They are especially similar in the early stages and are difficult to distinguish. For identification of these two species, I have included Table 4, which lists by larval stage the most readily observable differences for both species. In general, larvae of *P. goniurus* are smaller than those of *P. borealis*. In Stages I-III, *P. goniurus* larvae have fewer setae on the antennal scale and certain mouth parts than *P. borealis* larvae. From Stage IV to megalopa, the rostrum of *P. borealis* has more dorsal teeth, pereopod 2 is more developed, and the pleopods are fringed with more setae than larvae of *P. goniurus* (Haynes 1979).

with subterminal seta. Carapace usually with denticles on anteroventral margins in Stages I-V. Rostrum without teeth until Stage III; rostral tip bifid in Stage V. In Stage I, exopodites of maxillipeds 1, 2, and 3 with 5 or 6, 13 or 14, and 16 natatory setae, respectively; pereopods tucked under carapace; left mandible with a lacinia mobilis; basipodite of maxillule with 9 spinulose spines terminally; scaphognathite of maxilla with 12 setae along outer margin. Length: Stages I-VI, 6.5-20.2 mm. Range: Sea of Japan to Chukchi Sea to Columbia River mouth (northwestern United States); Barents Sea to North Sea; western Greenland to Gulf of Maine; depth, 16-1,380 m (Butler 1980).

Key III.—Larval and first juvenile stages of *Pandalus borealis* (see footnote 7 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae ..... Stage I
   Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 4 and 5 tucked under cephalothorax; uropods enclosed ..... Stage II
   Rostrum with ≥ 1 dorsal tooth at base; pereopods 4 and 5 extend ventrally; uropods free ... 3

3. Rostrum with 1 or 2 dorsal teeth at base; antennal flagellum with 8 segments and same length as scale; endopodite of uropod about 1/3 length of exopodite ..... Stage III
   Rostrum with ≥ 4 dorsal teeth; antennal flagellum with ≥ 15 segments and longer than scale; endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 4-8 dorsal teeth (usually 6), without ventral teeth; tip of rostrum styliform; pleopods with a few small setae at tip; endopodite of uropod about 2/3 length of exopodite ..... Stage IV
   Rostrum with > 8 dorsal teeth and ≥ 4 ventral teeth; tip of rostrum bifid; pleopods setose; endopodite of uropod nearly as long as expodite 5

5. Rostrum with 9-12 dorsal teeth and 4 or 5 small ventral teeth; carapace with supraorbital spine; telson with 2 spines on each lateral margin; lateral margins of telson nearly parallel ..... Stage V
   Rostrum with > 12 dorsal teeth and ≥ 6 distinct ventral teeth; carapace without supraorbital spine; telson with ≥ 4 spines on each lateral margin; lateral margins of telson taper posteriorly 6

6. Mandibles without palps; exopodites on maxillipeds and pereopods reduced in size; lateral margins of telson converge posteriorly but widen slightly at junction with posterior margin ..... Stage VI (megalopa)
   Mandibles with palps; vestigial exopodites on maxillipeds and pereopods; telson with lateral margins converging to narrow tip, as in adult ..... Stage VII (first juvenile)

***Pandalus danae* Stimpson**

Six larval stages.

Stage I, known parentage; Stages II-VI, from plankton; figures 3-5 in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; basipodite of maxillule without subterminal seta; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages developed; naked exopodites on pereopods 1 and 2; telson jointed with abdominal somite 6. Length: Stages I-VI, 5.7-17.0 mm. Range: Resurrection Bay, AK, to Point Loma, CA; depth, intertidal to 185 m (Butler 1980).

Key IV.—Larval stages of *Pandalus danae*.

1. Eyes sessile; carapace without supraorbital spine; exopodites on pereopods 1 and 2 without natatory setae ..... Stage I
   Eyes stalked; carapace with supraorbital spines; exopodites on pereopods 1 and 2 with natatory setae 2

2. Rostrum without teeth; uropods enclosed ... . Stage II
   Rostrum with teeth; uropods free 3

3. Rostrum with 2 or 3 minute dorsal teeth at base; endopodite of uropods noticeably shorter than exopodite ..... Stage III
   Rostrum with ≥ 8 teeth dorsally; endopodite of uropods same length as exopodite 4

4. Pleopods small, slightly cleft buds; telson widens slightly posteriorly ..... Stage IV

TABLE 4.—Morphological characteristics for distinguishing between larvae of *Pandalus borealis* and *P. goniurus* reared in situ in Kachemak Bay, Alaska (from Haynes 1979).

Stage and characteristic	*Pandalus borealis*	*Pandalus goniurus*
Stage I zoea:		
Mean total length	6.7 mm (range 6.5-7.3 mm; 25 specimens)	4.0 mm (range 3.7-4.2 mm; 10 specimens)
Number of plumose setae fringing antennal scale	19	9
Number of spines terminally on basipodite of maxillule	9	5
Number of plumose setae on scaphognathite (in addition to single proximal seta)	11	4
Number of natatory setae on each exopodite:		
maxilliped 1	5-6	4
maxilliped 2	13-14	8
maxilliped 3	16	12
Stage II zoea:		
Mean total length	7.5 mm (range 6.7-8.2 mm; 25 specimens)	5.9 mm (range 4.5-5.3 mm; 10 specimens)
Number of plumose setae fringing antennal scale	about 25	about 19
Number of natatory setae on each exopodite:		
maxilliped 1	7	6
maxilliped 2	16	12
maxilliped 3	18	14
pereopods 1, 2, 3	16, 16, 12	12, 8, 8
Stage III zoea:		
Mean total length	9.5 mm (range 9.0-10.0 mm; 10 specimens)	6.2 mm (range 6.0-6.6 mm; 10 specimens)
Rostrum	1-2 conspicuous teeth	1 inconspicuous tooth
Antennal flagellum	8-segmented	3-segmented
Antennal scale	about 30 setae	about 20 setae
Stage IV zoea:		
Mean total length	13.0 mm (range 12.6-13.2 mm; 10 specimens)	7.7 mm (range 6.8-8.3 mm; 10 specimens)
Rostrum	6-7 dorsal teeth	2 dorsal teeth
Antennal flagellum	about 1½ times length of scale, extending past tips of plumose setae	longer than scale but not extending past tips of plumose setae
Propodite of pereopod 2	projected anteriorly about 1/2 length of dactylopodite	projected anteriorly only slightly
Pleopods	segmented, pleopod 2 about 1/2 height of abdominal somite	unsegmented, pleopod 2 about 1/3 height of abdominal somite
Stage V zoea:		
Mean total length	16.0 mm (range 15.2-17.1 mm; 10 specimens)	10.3 mm (range 8.2-11.3 mm; 10 specimens)
Rostrum	9-12 dorsal teeth; tip bifid; 45 partially developed ventral teeth	5-6 dorsal teeth; tip not bifid (but may show slight protuberance); no ventral teeth
Chela of pereopod 2	fully formed	not fully formed, propodite extension about 1/2 length of dactylopodite
Pleopods	with appendix interna; fringed with plumose setae; 2 as long or longer than height of abdominal somite	without appendix interna; 2-4 simple setae terminally; pleopod 2 about 2/3 height of abdominal somite
Stage VI (megalopa):		
Mean total length	18.5 mm (range 17.4-20.2 mm; 5 specimens)	13.8 mm (range 11.1-15.8 mm; 6 specimens)
Rostrum	13-15 dorsal teeth, 6-7 ventral teeth	8-9 dorsal teeth, 4-5 ventral teeth

Pleopods distinct and biramous; sides of telson parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; exopodites on maxillipeds and pereopods have natatory setae . . . . . Stage V
Carapace without supraorbital spine; exopodites on maxillipeds and pereopods naked and vestigal . . . . . Stage VI (megalopa)

***Pandalus goniurus* Stimpson**
(see footnote 7)

Six larval stages.
Stages I-V, VI (megalopa), and VII (first juvenile), all from both known parentage and plankton; figures 1-7 in Haynes (1978a).
Stages I-VII from plankton; figure 2 in Makarov (1967).
Stage I, known parentage; figure 1 in Ivanov (1965).

In all stages, carapace and abdominal somites not flared laterally; subterminal seta on basipodite of maxillule. In Stages I-V, carapace usually with denticles on anteroventral margin. In Stage I, pereopods 1-5 tucked under carapace; exopodites of maxillipeds 1-3 with 4, 8, and 12 natatory setae, respectively; lacinia mobilis on left mandible; 5 spinulose spines terminally on basipodite of the maxillule; 5 setae along outer margin of scaphognathite of maxilla. Rostrum without teeth until Stage IV (in Stage III, rostrum with beginning of a tooth at base); rostral tip becomes bifid in Stage VI. Length: Stages I-VI, 3.7-15.8 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; 5-450 m (Butler 1980).

Key V.—Larval and first juvenile stages of *Pandalus goniurus* (see footnote 6 and Table 4).

1. Eyes sessile; pleopods absent; telson with 7 + 7 setae . . . . . Stage I
Eyes stalked; pleopods present as minute buds; telson with 8 + 8 setae 2

2. Rostrum without teeth; pereopods 3-5 tucked under cephalothorax; uropods enclosed . . . . . Stage II
Rostrum either with undeveloped or developed teeth; all pereopods extended ventrally; uropods free 3

3. Rostrum with undeveloped tooth at its base; antennal flagellum 3 segmented and about 2/3 length of scale; endopodite of uropod about 1/3 length of exopodite . . . . . Stage III
Rostrum with ⩾ 2 dorsal teeth; antennal flagellum with ⩾ 6 segments and longer than scale (not including setae); endopodite of uropod nearly same length as exopodite 4

4. Rostrum with 2 dorsal teeth; antennal flagellum does not extend beyond plumose setae of antennal scale; chela of pereopod 2 not formed; width of telson increases posteriorly . . . . . Stage IV
Rostrum with > 2 dorsal teeth; antennal flagellum extends beyond plumose setae of antennal scale; chela of pereopod 2 nearly or fully formed; lateral margins of telson nearly parallel or narrow posteriorly 5

5. Carapace with supraorbital spine; rostrum with 5 or 6 dorsal teeth, no ventral teeth; tip of rostrum styliform (may have undeveloped bifid tip); lateral margins of telson nearly parallel . . . . . Stage V
Carapace without supraorbital spine; rostrum with dorsal and ventral teeth; tip of rostrum bifid; lateral margins of telson narrow posteriorly 6

6. One or two setae between several posterior dorsal teeth of rostrum; 2-segmented mandibular palp without setae; exopodites of maxilliped 3 and pereopods present but reduced; carpopodite of left and right pereopods 2 with 20-25 and 7-9 joints, respectively . . . . . Stage VI (megalopa)
One or two setae between most, if not all, rostral teeth; 3-segmented mandibular palp with spiniform setae; no exopodites on maxilliped 3 and pereopods; carpopodites of left and right pereopods 2 with 29 and 11 joints, respectively . . . . . Stage VII

***Pandalus hypsinotus* Brandt**

Seven larval stages.
Stages I-VI, VII (megalopa), and VIII-IX (juveniles), known parentage; figures 1-6 in Haynes (1976).
Stage I, known parentage; Stages II-V, from plankton; figures 5-6 in Kurata (1964a).
Stage I, known parentage; Stages II and III, from

plankton; figures 6 (only Stage I figured) in Berkeley (1930).

In all described stages, carapace without denticles on anteroventral margin; posterior margins of abdominal somites without spinules. In Stage I, thoracic appendages segmented, dactyli undeveloped; naked exopodites on pereopods 1 and 2; telson not jointed with abdominal somite 6. Beginning in Stage III, basipodite of maxillule with subterminal seta; anal spine present. Length: Stages I-VII, 5.5-12.8 mm. Range: Sea of Japan to western Bering Sea; Norton Sound to Puget Sound, WA; depth, 5-460 m (Butler 1980).

Key VI.—Larval stages of *Pandalus hypsinotus*.

1. Eyes sessile; naked exopodites on pereopods ..... Stage I
   Eyes stalked; exopodites on pereopods with natatory setae 2

2. Rostrum without teeth; uropods enclosed ... . Stage II
   Rostrum with ⩾ 1 dorsal tooth at base; uropods free 3

3. Rostrum with dorsal tooth at base and no ventral teeth; exopodites on maxilliped and pereopods with natatory setae ..... Stage III
   Rostrum with ⩾ 11 dorsal teeth and ⩾ 2 small ventral teeth; naked, vestigial exopodites on maxillipeds and pereopods 4

4. Rostrum with 11-13 dorsal teeth and 2 or 3 small ventral teeth; tip of rostrum not bifid; mandibular palps unsegmented; telson margins nearly parallel but widen slightly posteriorly ..... Stage IV
   Rostrum with > 13 dorsal teeth and > 3 ventral teeth; tip of rostrum bifid; mandibular palp with 3 segments; telson slightly wider at midlength or narrows posteriorly 5

5. Bilobed pleopods without setae; telson slightly wider at midlength ..... Stage V
   Biramous pleopods with setae; telson narrows posteriorly 6

6. Carpopodite of left and right pereopods 2 with 19 and 7 or 8 joints, respectively; pleopods with setae only at tip; telson with 3 pairs of dorsolateral spines ..... Stage VI
   Carpopodite of left and right pereopods 2 with 24 or 25 and 10 joints, respectively; pleopods setose; telson with ⩾ 4 pairs of dorsolateral spines ..... Stage VII (megalopa)

***Pandalus jordani* Rathbun**

Thirteen larval stages.

Stages I-XIII, known parentage; figures 1-7 in Modin and Cox (1967).

Stages I-XIII, Stages XIV and XV (juveniles), all from both known parentage and plankton; figures 1-15 in Rothlisberg (1980).

Stages I-VIII, known parentage; figures 5-11 in Lee (1969).

In all described stages, carapace and abdominal somites not flared laterally and lack denticles or spinules; basipodite of maxillule without subterminal seta (except possibly Stage I). Pereopods tucked under carapace in Stage I. Rostrum without teeth in Stage I; rostrum with undeveloped dorsal tooth in Stage II; rostral tip bifid beginning at Stage VIII. Length: Stages I-XIII, 5.1-16.3 mm. Range: Unalaska, AK, to San Nicolas Island, CA; depth, 36-457 m (Butler 1980).

Key VII.—Larval and first juvenile stages of *Pandalus jordani*.

1. Eyes sessile; telson and abdominal somite 6 not jointed ..... Stage I
   Eyes stalked; telson and abdominal somite 6 jointed 2

2. Rostrum with precursor of first dorsal tooth; uropods enclosed ..... Stage II
   Rostrum with ⩾ 1 movable dorsal tooth; uropods free 3

3. Rostrum with 1 movable dorsal tooth; endopodite of uropod a bud with only a few setae ..... Stage III
   Rostrum with > 1 movable tooth; endopodite of uropod > 1/2 length of exopodite and setose 4

4. Posterior width of telson about twice anterior width ..... Stage IV
   Posterior width of telson noticeably less than twice anterior width 5

5. Lateral margins of telson widen slightly posteriorly ..... Stage V

Lateral margins of telson parallel or narrow posteriorly 6

6. Rostrum with 5 developed dorsal teeth and 1 undeveloped dorsal tooth; antennal flagellum with 15 segments and same length as scale . . . . . Stage VI
Rostrum with ≥ 5 developed dorsal teeth and > 1 undeveloped dorsal tooth; antennal flagellum with > 20 segments and longer than scale 7

7. Rostrum with 5 developed dorsal teeth and styliform tip; anal spine absent . . . . . Stage VII
Rostrum with > 5 developed teeth, tip of rostrum with precursor of subterminal tooth; anal spine present 8

8. Rostrum with 7 developed teeth; lateral margin of telson with 2 spines . . . . . Stage VIII
Rostrum with > 7 developed teeth; lateral margin of telson with ≥ 3 spines 9

9. Rostrum with 9 developed teeth; inner flagellum of antennule with 3 segments; outer flagellum of antennule with 2 segments . . . . . Stage IX
Rostrum with > 9 developed teeth; inner flagellum of antennules with ≥ 4 segments; outer flagellum of antennule with 3 segments 10

10. Rostrum with 10 developed teeth; medial pair of terminal telsonic spines shorter than adjacent pair . . . . . Stage X
Rostrum with > 10 developed teeth; medial pair of terminal telsonic spines same length or longer than adjacent pair 11

11. Inner flagellum of antennule with 4 segments; medial pair of terminal telsonic spines same length as adjacent pair . . . . . Stage XI
Inner flagellum of antennule with 5 segments; medial pair of terminal telsonic spines longer than adjacent pair 12

12. Rostrum with 12 developed dorsal teeth and precursors of 3 ventral spines; terminal margin of telson straight . . . . . Stage XII
Rostrum with > 12 developed dorsal teeth and precursors of > 3 ventral teeth; terminal margin of telson convex 13

13. Carapace with supraorbital spine; pereopod 2 with unsegmented carpus . . . . . Stage XIII (last larval stage)
Carapace without supraorbital spine; pereopod 2 with segmented carpus . . . . . Stage XIV (first juvenile stage)

***Pandalus kessleri* Czerniavski**

Four larval stages.

Stages I-IV and Stage V (first juvenile), known parentage; figures 2-6 (fig. 6, first juvenile stage) in Kurata (1955). (Stages II-IV have a mixture of zoeal and megalopal characters.)

Abbreviated larval development. In all described stages, carapace without denticles along anteroventral margin; antennal scale not jointed at tip; 2 lateral setae proximally on exopodite of maxilliped 1. Stages II and III with transverse dorsal groove. Rostrum with teeth beginning in Stage II. Supraorbital spines in Stage II only. In Stage I, antennal flagellum 3/4 length of body; antennal flagellum segmented throughout its length; telson with 30-34 setae; anal spine present; zoea longer than 8.1 mm. In Stage III, mandible with unjointed palp. Vestigial exopodites on pereopods 1 and 2 in Stages I and II. Pleopods with plumose setae in Stage II. Length: Stages I-IV, 8.1-10.8 mm. Range: Hokkaido, Japan (no depth given) (Kurata 1955).

Key VIII.—Larval and first juvenile stages of *Pandalus kessleri*.

1. Rostrum without teeth; eyes sessile . . . . Stage I
Rostrum with teeth, eyes stalked 2

2. Mandible without palp; uropods enclosed; carapace with supraorbital spine . . . . . Stage II
Mandible with palp; uropods free; carapace without supraorbital spine 3

3. Rostral tip not bifid; telson widens posteriorly . . . . . Stage III
Rostral tip bifid; telson margins parallel or narrows posteriorly 4

4. Mandibular palp unsegmented; sides of telson parallel; telson with 2 pairs of lateral spines and 11-14 terminal seta . . . . . Stage IV
Mandibular palp segmented; telson narrows posteriorly; telson with 3 pairs of lateral spines and several terminal setae vestigial as hairs . . . . . Stage V (first juvenile)

Pandalus platyceros **Brandt**

Five larval stages.

Stages I-V and Stages VI-X (juveniles), known parentage; figures 1-6 in Price and Chew (1972).

Stage I, known parentage; Stages II, IV?, and V?, from plankton; figures 9 and 10 in Berkeley (1930).

In all described stages, rostrum with teeth, basipodite of maxillule without subterminal seta. In Stages I-III, carapace flares laterally, lateral margins with denticles; abdominal somites flare laterally, lateral margins with spinules (Fig. 5). In Stage I, pleopods present as buds; telson jointed with abdominal somite 6. In Stages II and III, less flaring of abdominal somites and smaller denticles and spinules than in Stage I. Thoracic appendages developed in Stage I, except naked endopodites on pereopods 1-3. Length: Stages I-V, 8.1-13.0 mm. Range: Sea of Japan, Hokkaido; Unalaska Island, AK, to off San Diego, CA; depth, intertidal to 487 m (Butler 1980).

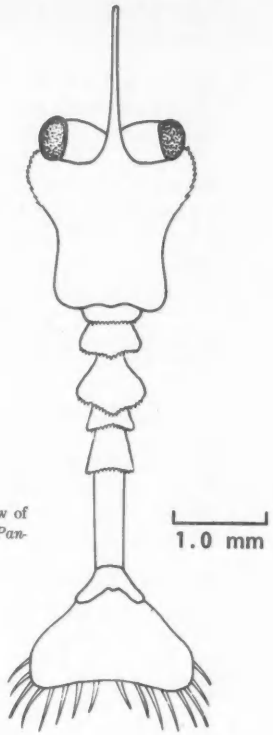

FIGURE 5.—Dorsal view of body, Stage I zoea of *Pandalus platyceros*.

Key IX.—Larval and first juvenile stages of *Pandalus platyceros*.

1. Rostrum without ventral teeth (Fig. 6); eyes sessile; pereopods with naked exopodites ..... Stage I
   Rostrum with ventral teeth; eyes stalked; pereopods with setose exopodites 2

2. Antennal flagellum with 6 segments and flagellum only slightly longer than plumose setae of scale; uropods enclosed ..... Stage II
   Antennal flagellum with ≥ 15 segments and flagellum at least twice length of scale; uropods free 3

3. Antennal flagellum about twice length of antennal scale; telson widens posteriorly; telson with 1 pair of lateral spines .... Stage III
   Antennal flagellum ≥ 3 times length of antennal scale; telson margins parallel or converge posteriorly; telson with > 1 pair of lateral spines 4

4. Carapace with supraorbital spines; mandibles without palps; pereopod 2 with unsegmented carpopodite; telson with 2 pairs of lateral spines ..... Stage IV
   Carapace without supraorbital spines; mandibles with palps; pereopod 2 with segmented carpopodite; telson with ≥ 3 pairs of lateral spines 5

5. Telson margins nearly parallel, distal margin concave ..... Stage V (megalopa)

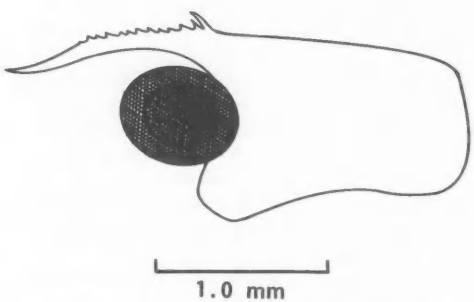

FIGURE 6.—Rostrum, Stage I zoea *Pandalus platyceros*.

Telson narrows posteriorly, distal margin convex ..... Stage VI
(first juvenile stage)

***Pandalus prensor* Stimpson**

Five larval stages.
Stages I-V (larvae) and VI-IX (juveniles), known parentage; figures 2-7 in Mikulich and Ivanov (1983).

Abbreviated larval development characterized by marked heterochrony in development of appendages. In all described stages, supraorbital spine absent; antennal flagellum segmented; antennal scale not jointed at tip; pereopods developed. In Stage I, rostrum curves ventrally between eyes; telson discoid and jointed with abdominal somite 6; natatory setae on exopodites of maxillipeds 1-3 and pereopods 1-2. Length: Stages I-V, carapace length 1.42-1.75 mm. Range: coastal waters of southern Okhotsk Sea, Sea of Japan, and southeastern Siberia (Vladivostok and Possjet Bay); depth, 2-93 m (Holthuis 1976; Mikulich and Ivanov 1983).

Key X.—Larval stages of *Pandalus prensor*.

1. Eyes sessile; rostrom bends ventrally between eyes ..... Stage I
   Eyes stalked; rostrom straight 2

2. Rostrum does not extend to anterior margin of eye; telson discoid; uropods enclosed ..... Stage II
   Rostrum extends beyond anterior margin of eye; telson rectangular; uropods free 3

3. Pleopods uniramous and unsegmented; telson with 7 pairs of terminal spines .... Stage III
   Pleopods (pairs II-V) biramous and segmented; telson with ⩽ 5 pairs of terminal spines ... 4

4. Ventral rostrum with 4 teeth; telson with 5 pairs of terminal spines ..... Stage IV
   Ventral rostrum with 6 teeth; telson with 3 pairs of terminal spines ..... Stage V

***Pandalus stenolepis* Rathbun**

Six larval stages.
Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figures 1 and 2 in Needler (1938); figure 73 in Gurney (1942; Page 208 verifies subterminal seta on maxillule).

In Stages I-IV, carapace flares laterally, lateral margin with denticles; abdominal somites with spinules and flared laterally. Flaring, size of denticles, and spinules decrease in Stages II-IV. In Stage I, pereopods tucked under carapace; telson not jointed with abdominal somite 6; and flagellum of antenna longer than antennal scale. Pleopods absent until Stage III. Length: Stages I-VI, 6.0-14.0 mm. Range: Unalaska Island, AK, to Hecata Bank, OR; depth, 49-229 m (Butler 1980).

Key XI.—Larval and first juvenile stages of *Pandalus stenolepis*.

1. Eyes sessile; rostrum without teeth .... Stage I
   Eyes stalked; rostrum with teeth 2

2. Rostrum with only dorsal teeth (4-5 teeth); uropods enclosed ..... Stage II
   Rostrum with dorsal and ventral teeth; uropods free 3

3. Rostrum with 8 or 9 dorsal teeth and 2 ventral teeth; pleopod buds only slightly cleft ..... Stage III
   Rostrum with > 9 dorsal teeth and > 2 ventral teeth; pleopods biramous 4

4. Unjointed pleopods without setae .... Stage IV
   Jointed pleopods with setae 5

5. Right and left pereopods 2 with endopodites of same length; pleopods with a few setae; each endopodite without an appendix interna (Fig. 1N, ai) ..... Stage V
   Right and left pereopods 2 with endopodites of different lengths; pleopods setose; each endopodite with an appendix interna 6

6. Carapace with supraorbital spine; setose exopodite on each pereopod ..... Stage VI
   (megalopa)
   Carapace without supraorbital spine; naked, vestigial exopodite on each pereopods ..... Stage VII
   (first juvenile stage)

***Pandalus tridens* Rathbun**

Probably 8 larval stages.
Stage I, known parentage; Stages I-VII, from plankton; figures 1-7 in Haynes (1976).
Stage I, known parentage; figure 1 in Ivanov (1971).

In all described stages, carapace and abdominal somites not flared laterally; antennal scale relatively long and narrow (about 5-7 times as long as wide). In Stages I-III, but rarely in Stage IV, carapace with denticles along anteroventral and posteroventral margins; posterior margin of abdominal somites 1-5 fringed with spinules (Fig. 7). Rostrum sinuate, projects somewhat upwards in Stages I-III, remains shorter than carapace as late as Stage VIII, without teeth until Stage IV. Antennal flagellum shorter than antennal scale through at least Stage V. Length: Stages I-VII, 3.1-13.0 mm. Range: Bering Sea to San Nicolas Island, CA; depth, 5-1,984 m (Butler 1980).

Key XII.—Larval stages (Stages I-VII) of *Pandalus tridens*.

1. Eyes sessile; carapace without supraorbital spine; pereopods 1-3 without exopodites; telson with 7 + 7 setae ..... Stage I
   Eyes stalked; carapace with supraorbital spine; exopodites on pereopods 1-3; telson with 8 + 8 setae 2

2. Uropods enclosed ..... Stage II
   Uropods free 3

3. Endopodite of uropod < 1/2 length of exopodite ..... Stage III
   Endopodite of uropod > 1/2 length of exopodite 4

4. Rostrum with 2 dorsal teeth; endopodite of uropod about 3/4 length of exopodite; telson widens posteriorly ..... Stage IV
   Rostrum with > 2 dorsal teeth; endopodite of uropod nearly same length as exopodite; lateral margins of telson nearly parallel 5

5. Antennal flagellum with 5 segments and about 2/3 length of antennal scale; chela of pereopod 2 slightly developed (Fig. 8); pleopod 2 about 1/4 height of abdominal somite 2 ..... Stage V
   Antennal flagellum with ≥ 20 segments and as long as or longer than antennal scale; chela of pereopod 2 well formed (Fig. 9); pleopods 2 at least 1/2 height of abdominal somite 2 6

6. Rostrum with 6 dorsal teeth; pleopods without setae; telson slightly wider near center ..... Stage VI

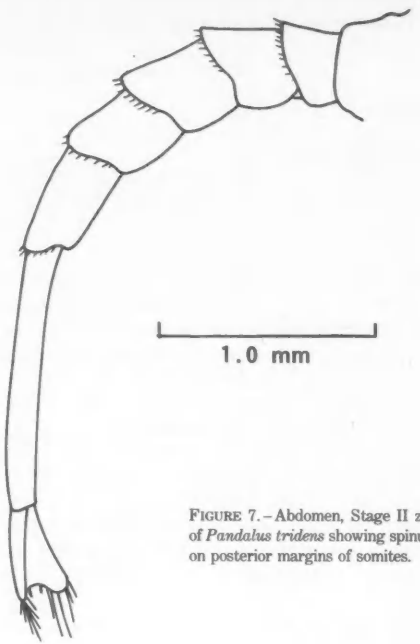

FIGURE 7.—Abdomen, Stage II zoea of *Pandalus tridens* showing spinules on posterior margins of somites.

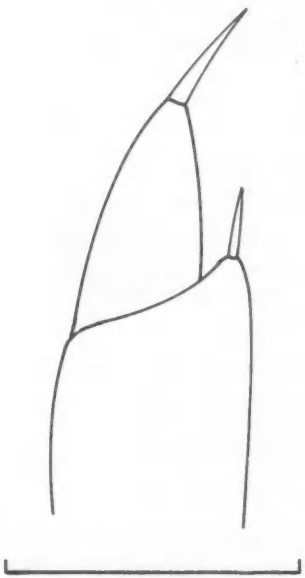

FIGURE 8.—Chela of pereopod 2, Stage V zoea of *Pandalus tridens*.

Rostrum with 7 dorsal teeth; pleopods tipped with a few setae; telson margins nearly parallel ..... Stage VII

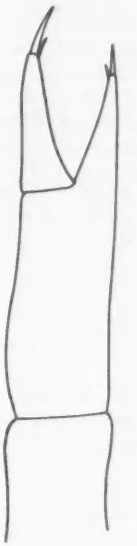

FIGURE 9.—Chela of pereopod 2, Stage VI zoea of *Pandalus tridens*.

HIPPOLYTIDAE

(Genera *Eualus*, *Heptacarpus*, *Hippolyte*, *Lebbeus*, and *Spirontocaris*)

In all described stages, rostrum absent to long, usually spiniform (slightly sinuate in species with abbreviated development); plumose seta rather than long setose spine on inner flagellum of antennule; exopodites on pereopods 1-2, 1-3, or 1-4; abdomen without dorsal spine or keels on somite 3 (megalopa of *Spirontocaris spinus* with a minute dorsoposterior spine on abdominal somite 3); posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5 (spines may be lacking in megalopa); pereopod 1 never subchelate; anal spine present in all stages (exception: at least Stage I of *Hippolyte*). Rostrum may have teeth in last zoeal stage (megalopa); supraorbital spine usually absent in Stage I. Stages I-III, antennal scale nearly always jointed or partially jointed at tip. Stage I, exopodites of maxilliped 1-3 with 4, 5, 5 natatory setae; about Stage V, setose setae on endopodite of each pleopod; telson does not widen posteriorly, has more than 1 pair of lateral spines.

The principal morphological characters and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean are summarized in Table 5.

TABLE 5.—Principal morphological characteristics and number of larval stages of known larvae of hippolytid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Supra-orbital spine in Stage I	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Postero-lateral spines on abdominal somites	Telsonic spines in Stage I	No. of larval stages
Eualus barbatus	–	–	–	?	–	7 + 7	?
E. fabricii	+	–	[1]5	1-3	4, 5	7 + 7	?
E. gaimardii	+	–	[1]4	1-3	5	7 + 7	6
E. herdmani	–	–	–	?	–	7 + 7	?
E. macilentus	+[2]	–	–	?	–	7 + 7	?
E. pusiolus	+[2]	?	–	1-4	–	7 + 7	6-7
E. suckleyi	+	–	[1]5	1-3	5	7 + 7	?
Heptacarpus brevirostris	–	–	–	?	–	7 + 7	?
H. camtschaticus	+[2]	–	[1]5	1, 2	–	7 + 7	?
H. paludicola	–	–	–	?	–	7 + 7	?
H. tridens	–	–	–	?	–	7 + 7	?
Hippolyte clarki	+	–	[1]1	?	5	7 + 7	?
Lebbeus groenlandicus	+	–	5	–	4, 5	9(10) + 10(11)	3
L. polaris	+	–	5	–	4, 5	9 + 9	4
Spirontocaris arcuata	+	–	[1]5	1, 2	–	7 + 7	?
S. lilljeborgii	+	+	[1]5	1, 2	4	7 + 7	6
S. murdochi	+	–	[1]5	1, 2	4, 5	7 + 7	?
S. ochotensis	–	+	[1]5	1, 2	4, 5	7 + 7	?
S. phippsii	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus	+	+	[1]5	1, 2	4, 5	7 + 7	6
S. spinus var. *intermedia*	+	–	[1]5	1, 2	4, 5	7 + 7	?

[1]Undeveloped pereopods. [2]Minute.

Genus *Eualus* Thallwitz

In Stage I, rostrum absent to long; carapace without supraorbital spine; tip of antennal scale jointed; pereopods absent or, if present, undeveloped; anal spine present. Exopodites first appear on pereopods 1-3 or 1-4 in Stage III. Posterolateral spines absent, on abdominal somites 4 and 5, or only on abdominal somite 5.

***Eualus barbatus* (Rathbun)**

Only Stage I described, known parentage; figure 3 in Ivanov (1971).

Carapace without rostrum, supraorbital spine, or denticles; pereopods absent; abdominal somites without posterolateral spines or denticles but with isolated hairs on dorsal surface of abdominal somites 3 and 4; abdominal somite 3 with indistinct row of setae on dorsal surface. Length: 4.5 mm. Range: Pribilof Islands, AK, to Hecata Bank, OR; depth, 82-507 m (Butler 1980).

***Eualus fabricii* (Krøyer)**

Only Stages I and II described, known parentage; figure 5 in Haynes (1981).

Not "*Spirontocaris* larva Nr. 3, *Spirontocaris fabricii*?" as described by Stephensen (1916) (see Haynes 1981).

Not "*Spirontocaris*-larvae No. 3? *Spirontocaris fabricii* (Krøyer)" as described by Stephensen (1935) (see Haynes 1981).

Not *Spirontocaris fabricii* as described by Frost (1936) (see Haynes 1981).

Not "*Eualus fabricii* (Krøyer)" as described by Pike and Williamson (1961) (see Haynes 1981).

In all stages, posterolateral spines on abdominal somites 4 and 5. In Stage I, antennal flagellum about 1.5 times length of antennal scale; minute spinules along dorsoposterior margins of abdominal somites 4 and 5 (spinules absent in Stage II); supraorbital spine absent (small in Stage II). In Stages I and II, pereopods 1-3 with undeveloped exopodites. In Stage II, exopodites of maxillipeds 1-3 with 4, 9, and 11 natatory setae, respectively; telson not jointed with abdominal somite 6. Length: Stages I and II, 3.5-4.3 mm. Range: Sea of Japan, Okhotsk Sea; Chukchi Sea to British Columbia; in northwestern Alantic, from Foxe Basin and West Greenland to Massachusetts Bay (eastern United States); depth, 4-255 m (Butler 1980).

***Eualus gaimardii* (H. Milne Edwards)**

Six larval stages.

Stages I-VI, known parentage; also Stages I and II from plankton; figure 2 in Pike and Williamson (1961).

Last zoeal stage from plankton, described as "Spirontocaris-larva No. 2A" by Stephensen (1935), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198). No figure.

Stage V (?), described as "*Spirontocaris* B" by Frost (1936), probably *E. gaimardii* forma *gibba* (see Pike and Williamson 1961, p. 198); figure 4 in Frost (1936).

Stage I, known parentage; described as *Spirontocaris gaimardii* by Lebour (1940); figure 1 in Lebour (1940).

Stage I, known parentage; figures 21-23 in Williamson (1957a: figures from Lebour 1940).

In all described stages, rostrum long (about 1/3 carapace length); no subterminal seta on maxillule. Rostrum without teeth until Stage V. In Stage V, rostrum with 2 dorsal teeth; in Stage VI, rostrum with 3 dorsal teeth. Supraorbital spine in Stages II-V. Carapace with 3 or 4 denticles on anteroventral margin in Stages I-IV. Antennal flagellum does not extend beyond antennal scale until Stage V. Natatory setae on exopodites of maxillipeds 1-3: 5, 7, 7 natatory setae, respectively, in Stage II; 5, 9, 9 in Stage III; and 5, 10, 10 in Stages IV and V. In Stages I-V, posterolateral spine on abdominal somite 5. Length: Stages I-VI, 2.9-5.4 mm. Range: circumpolar, southward to North Sea; Cape Cod, MA; Sitka, AK; Siberia; depth, 10-900 m (Holthuis 1947).

***Eualus herdmani* (Walker)**

Only Stage I described, known parentage; described as "*Spirontocaris herdmani*" by Needler (1934). No figure.

Stage I, known parentage; Pike and Williamson (1961: description from Needler 1934). No figure.

Carapace without rostrum or supraorbital spine but with 3 anteroventral denticles; abdomen without posterolateral spines; anal spine minute. No length given. Range: Sitka, AK, to Puget Sound, WA; depth, 18-232 m (Butler 1980).

***Eualus macilentus* (Krøyer)**

Only Stage I described, known parentage; figure 2 in Ivanov (1971).

No supraorbital spine; 4 denticles on anteroventral margin of carapace; pereopods absent; abdomen without spines or denticles. Length: 3.0 mm. Range: West Greenland to Nova Scotia; Bering and Okhotsk Seas; depth, 150-540 m (Holthuis 1947).

Eualus pusiolus **(Krøyer)**

Larvae described from Atlantic specimens.
Seven or eight larval stages.
Stage I, known parentage; Stages I-VII, from plankton; figure 3 in Pike and Williamson (1961).
Last zoeal stage, from plankton, described as "*Spirontocaris* C" by Frost (1936); figure 5 in Frost (1936).
Stage I, known parentage; described as "*Spirontocaris pusiola*" by Bull (1938); figure 1 in Bull (1938).
Stage I, known parentage; figures 27-30 in Williamson (1957a); figures from Bull (1938).

In all described stages, 3 denticles on anteroventral margin of carapace; no spines, denticles, or dorsal setae on abdominal somites. Rostrum minute in Stage I, only slightly larger in other stages, without teeth in all stages. Exopodites of maxillipeds 1-3, with 5, 8, and 8 natatory setae, respectively, in Stage II. In Stages V-VIII, pereopods 1-4 with setae. Length: Stages I-VIII, 2.2-4.8 mm. Range: Sea of Japan to Chukchi Sea and British Columbia; Gulf of St. Lawrence to Cape Cod, MA; Europe from the southwestern Barents Sea to Spain; depth, intertidal to 1,381 m (Butler 1980).

Eualus suckleyi **(Stimpson)**

Only Stages I and II described, known parentage; figures 3 and 4 in Haynes (1981).

In Stage I, anteroventral margin of carapace with 3 or 4 denticles; undeveloped exopodites on pereopods 1-3. In Stage II, carapace with supraorbital spine, without denticles along anteroventral margin. In Stage II, maxillipeds 1-3 with 4, 5, and 5 natatory setae, respectively; pereopods 1-5 present but undeveloped. Length: Stage I, 3.0-3.5 mm; Stage II, 3.5-4.2 mm. Range: Okhotsk Sea to Chukchi Sea to about Grays Harbor, WA; depth, 11-1,025 m (Butler 1980).

Genus *Heptacarpus* Holmes

Only Stage I described. Rostrum minute to absent; no supraorbital spine; pereopods absent or pairs 1-5 present but undeveloped; abdominal somites without posterolateral spines; exopodites develop on pereopods 1 and 2; tip of antennal scale not always jointed.

Heptacarpus brevirostris **(Dana)**

Stage I, known parentage; described as *Spirontocaris brevirostris* by Needler (1934). No figures.

Carapace without anteroventral spines; antennal scale partially jointed at tip. Length: Stage I, 1.5 mm. Range: Aleutian Islands, AK, to San Francisco Bay, CA; depth, intertidal to 128 m (Butler 1980).

Heptacarpus camtschaticus **(Stimpson)**

Stage I, known parentage; figure 8 in Haynes (1981).

Carapace without spines; minute rostrum curves slightly downward following dorsal contour of eyes; undeveloped exopodites on pereopods 1 and 2; abdomen without spines or spinules. Length: Stage I, 2.9 mm. Range: Sea of Japan to Chukchi Sea and Strait of Georgia, WA; depth, intertidal to 108 m (Butler 1980).

Heptacarpus paludicola **(Holmes)**

Stage I, known parentage; described as *Spirontocaris paludicola* by Needler (1934); figure 1 in Needler (1934).

Antennal scale partially jointed at tip; abdomen without posterolateral spines. Length: Stage I, 2.0 mm. Range: Tava Island, AK, to San Diego, CA; depth, intertidal to 10 m (Butler 1980).

Heptacarpus tridens **(Rathbun)**

Stage I, known parentage; described as *Spirontocaris tridens* by Needler (1934); figure 1 in Needler (1934).

Carapace without anteroventral spines; antennal scale unsegmented. Length: Stage I, 3.0 mm. Range: Aleutian Islands, AK, to Cape Flattery, WA; depth, intertidal to 110 m (Butler 1980).

Genus *Hippolyte* Leach

Only Stage I described. Antennal scale without joints at tip.

***Hippolyte clarki* Chace**

Stage I, known parentage; described as *Hippolyte californiensis* by Needler (1934); figure 1 in Needler (1934).

Rostrum long; carapace with 4 anteroventral denticles; bud of pereopod 1 present; small posterolateral spines on abdominal somite 5. Length: 1.9 mm. Range: Sheep Bay, AK, to Puget Sound, WA; Santa Catalina Island, CA; depth, intertidal to 30.5 m (Butler 1980).

Genus *Lebbeus* White

In all described stages, posterolateral spines on abdominal somites 4 and 5 (Fig. 2). In Stage I, larvae relatively long (> 5.0 mm); rostrum long, slightly sinuate (Fig. 2), with no supraorbital spine. Abbreviated development.

***Lebbeus groenlandicus* (Fabricius)**

Three larval stages.
Stages I-III from both known parentage and plankton; figures 1-3 in Haynes (1978b).
Stage I, known parentage; figure 5 in Ivanov (1971).
Not "*Spirontocaris*-larva No. 1A." as described by Stephensen (1935) (see Haynes 1978b).

Somewhat more developed in each stage than larvae of *L. polaris*. In Stage II, no vestigial exopodites on pereopods. Telson with about 20 setae in Stages I and II, and 3 + 3 spines in Stage III (megalopa). Length: 6.4-7.6 mm. Range: Sea of Japan to Chukchi Sea to Puget Sound, WA; arctic coast of Canada; Greenland to Cape Cod, MA; depth, 11-518 m (Butler 1980).

***Lebbeus polaris* (Sabine)**

Probably 4 larval stages.
Stages I and II, known parentage; figures 1 and 2 in Haynes (1981).
Neither *Spirontocaris polaris* (= *L. polaris*) as described by Stephensen (1916) nor "*Spirontocaris*-larva No. 1" as described by Stephensen (1935) (see Haynes 1981).

In Stages I and II, telson with 9 + 9 setae. In Stage II, vestigial exopodite on peropod 1. Length: Stage I, 5.2 mm; Stage II, 5.8 mm. Range: circumpolar, southward to the Skagerrak and Hebrides; Cape Cod, MA; Bering and Okhotsk Seas; Aleutian Islands, AK; depth, 0-930 m (Holthuis 1947).

Genus *Spirontocaris* Bate

In all described stages, rostrum absent to long; posterolateral spines on abdominal somites 4 and 5, or 5 only; no minute spines on posterior margins of abdominal somites. In Stage I, supraorbital spine present or absent; all pereopods present but undeveloped. Exopodites only on pereopods 1 and 2 in later stages (usually by Stage IV or V).

***Spirontocaris arcuata* Rathbun**

Only Stage I described, known parentage; figure 6 in Haynes (1981).

Rostrum short (about 1/7 carapace length), projects downward following contour of eyes; 2 or 3 minute denticles on anteroventral margin of carapace; supraorbital spine absent; posterolateral spines on abdominal somites 4 and 5. Length: 4.1-4.4 mm. Range: Sea of Japan to Chukchi Sea to Juan de Fuca Strait, WA; Canadian Arctic; depth, 5-641 m (Butler 1980).

***Spirontocaris lilljeborgii* (Danielssen)**

Larvae described from Atlantic Ocean.
Six larval stages.
Stages I and II, known parentage; Stages I-V, from plankton; Stages VI (megalopa) and VII (first juvenile), reared in laboratory from Stage V; figure 1 in Pike and Williamson (1961).
Stage I, known parentage; described as *S. spinus* var. *lilljeborgi* by Lebour (1937); figure 1 in Lebour (1937).
Stage I; figures 14-16 in Williamson (1957a). Description and figures from Lebour (1937).

In all described stages, posteroanterior margins of carapace smooth; abdominal somite 4 with a dorsal tuft of short setae, without posterolateral spines. Rostrum long (about 3/4 length of antennular peduncle), deepens slightly in later stages but does not develop teeth until megalopa. Supraorbital spine rudimentary in Stage I, clearly defined in later stages. Posterolateral spines on abdominal somite 5 becoming smaller in later stages and may be absent in Stages V and VI. Megalopa and first juvenile stage without dorsal tooth on posterior margin of abdominal somite 3. Length: Stages I-VI, 4.8-8.5 mm. Range: From Spitsbergen and southwestern

Barents Sea south to south coast of England; Iceland; Greenland; east coast of North America from Nova Scotia to Massachusetts Bay; arctic Alaska; depth, 20-1,200 m (Holthuis 1947).

***Spirontocaris murdochi* Rathbun**

Only Stages I-III described, known parentage; figures 1-3 in Haynes (in press).

Rostrum about 1/4 carapace length, supraorbital spine in Stage III; posterolateral spine on abdominal somite 5 longer than posterolateral spine on abdominal somite 4; dorsal surface of abdominal somite 4 without tuft of setae. Length: Stages I-III, 3.2-4.3 mm. Range: Arctic to southeastern Alaska, Kamchatka, Sea of Okhotsk, Patience Bay (Sakhalin); depth, 18-50 m (Holthuis 1947; Haynes in press).

***Spirontocaris ochotensis* (Brandt)**

Only Stage I described, known parentage; figure 7 in Haynes (1981).

No rostrum; carapace usually with only 1 denticle along anteroventral margin; supraorbital spine minute; posterolateral spines on abdominal somites 4 and 5. Length: 2.8 mm. Range: Sea of Japan to Bering Sea and western coast of Vancouver Island, British Columbia; depth, intertidal to 247 m (Butler 1980).

***Spirontocaris phippsii* (Krøyer)**

Larvae known from Atlantic Ocean.

Stage II, from plankton; Pike and Williamson (1961). No figure. Identity assumed from distribution of adults.

Stage III, from plankton; described as "*Spriontocaris*-larva Nr. 2," ("*Sp. turgida*?"); figure 6 in Stephensen (1916). Not figure 7 in Stephensen (1916), "last stage"; probably *Eualus macilentus* (see Pike and Williamson 1961) (Pike and Williamson identified figure 7 as *E. macilentus* based on identity of *S. spinus* and *S. lilljeborgii* and distribution of *Eualus* spp. in Greenland waters).

Stage V, from plankton; described as "*Spirontocaris*-larva No. 2 (? *Sp. turgida* (Krøyer))" and "*Spirontocaris*-larva No. 2B" in Stephensen (1935) (see Pike and Williamson 1961 for identification).

Spines on abdominal somites 4 and 5; abdominal somite 4 without dorsal tuft of setae. Length: Stage II, 6.0 mm. Range: circumpolar, southward to northern Norway; Cape Cod, MA; Shumagin Islands, AK; and Plover Bay, Siberia; depth, 11-225 m (Holthuis 1947).

***Spirontocaris spinus* (Sowerby)**

Larvae described from Atlantic Ocean only.

Six larval stages.

Stages I and II, known parentage; Stages III-VII (Stage VII, first juvenile), from plankton; figure 1 in Pike and Williamson (1961).

Stage IV, from plankton; described as "*Spirontocaris* A" by Frost (1936); figure 3 in Frost (1936) (see Pike and Williamson 1961 for identification).

Stage I, probably from known parentage; Stage V, probably from plankton (see Pike and Williamson 1961); figures 17-20 in Williamson (1957a).

Larvae and juvenile stages very similar to those of *S. lilljeborgii*. In all described stages, abdominal somite 4 with a dorsal tuft of short setae; abdominal somites 4 and 5 with posterolateral spines; posterolateral spines on abdominal somite 5 remain same size in all zoeal stages. Posterior margin of abdominal somite 3 with distinct dorsal tooth in megalopa and first juvenile stage. Length: Stages I-VI, 4.3-8.0 mm. Range: Circumpolar, southward to the northern North Sea, Massachusetts Bay (eastern United States), Alaska Peninsula, and eastern coast of Siberia; depth, 16-400 m (Holthuis 1947).

***Spirontocaris spinus* var. *intermedia* Makarov[8]**

Only Stage I described, known parentage; figure 4 in Ivanov (1971).

Not *S. spinus intermedia* as described by Makarov (1967) (see Ivanov 1971).

Rostrum long (> 1/3 carapace length); no supraorbital spine; abdominal somite 4 with dorsal tuft of setae; posterolateral spines on abdominal somites 4 and 5. Length: Stage I, 5.0 mm. Range: (see *S. spinus*); depth, 9-1,380 m (Hayashi 1977).

[8]According to Ivanov (1971), V. V. Makarov, rather than Z. I. Kobjakova, is the author of the subspecies *S. spinus* var. *intermedia* based on Article 51(c) of Chapter XI of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1964). The subspecies *S. spinus* var. *intermedia*, however, may be identical to *S. spinus*. Hayashi (1977) believed that the morphological criteria used by Kobjakova (1937) to distinguish *S. spinus* var. *intermedia* from *S. spinus* were too small and variable to be valid.

CRANGONIDAE

(Genera *Argis*, *Crangon*, *Mesocrangon*, *Paracrangon*, *Sabinea*, and *Sclerocrangon*)

Rostrum nearly always present and long (at least 1/4 length of carapace), spiniform, and always without teeth (rostrum spinulose in Stage I larvae of *Paracrangon echinata*); supraorbital spine absent; inner flagellum of antennule a setose spine or oblong projection rather than a plumose seta; tip of antennal scale never segmented; exopodite usually only on pereopod 1 (rarely on pereopod 2); maxillule without subterminal seta on basipodite; dorsal spine may be on abdominal somite 3 or keels on both abdominal somites 2 and 3; usually posterolateral spines on abdominal somite 5; endopodite of pleopods undeveloped; usually telson widens posteriorly, never with more than 1 pair of lateral spines. Pereopods 1 subchelate at about Stage V. Anal spine absent until about Stage IV.

The principal morphological characters and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean are summarized in Table 6.

Genus *Argis* Krøyer

In Stage I, rostrum styliform; pereopods and pleopods developed but not functional; exopodite on pereopod 1 rudimentary or absent; abdominal somite 3 without dorsal spine; abdominal somite 5 with posterolateral spine (posterolateral spine absent in megalopa of *A. dentata*).

***Argis crassa*[9] (Rathbun)**

Only Stage I described, known parentage; figure 2 in Ivanov (1968).

Not Stage I *A. crassa* as described by Makarov (1967) in figure 21.

Antennal scale without distal spine on outer margin; endopodite of maxillule with 5 setae; scaphognathite of maxilla with 9 setae; abdominal somites 2-5 fringed dorsally with small spinules; telson and abdominal somite 6 jointed; telson with 8 + 8 setae. Length: 7.5 mm. Range: Sea of Japan to Bering Sea to San Juan Islands, WA; depth, 4-125 m (Butler 1980).

***Argis dentata* (Rathbun)**

Three larval stages. Stage I described, known parentage from Pacific Ocean; Stage I-III described, from plankton from Atlantic Ocean.

Stages I-III, from plankton; figures 1-6 in Squires (1965).

Stage I, known parentage; figure 3 in Ivanov (1968).

Megalopa, from plankton; described as "*Necto-*

[9]Makarov (1967) described a crangonid larva from plankton that has a short rostrum flattened dorsoventrally. He assumed it was *Argis* (= *Nectocrangon*) *crassa*. According to Ivanov (1968), who reared Stage I *A. crassa* from known parentage, the larva described by Makarov is neither *Argis crassa* nor a later stage of *Argis crassa*. The short flattened rostrum, however, is typically a postlarval (juvenile) characteristic of crangonid shrimp. The specimen described by Makarov, therefore, is probably a juvenile rather than a larva.

TABLE 6.—Principal morphological characteristics and number of larval stages of known larvae of crangonid shrimp of the northern North Pacific Ocean. + = yes; – = no; ? = unknown.

Species	Rostrum	Pereopods in Stage I	Pereopods bearing an exopodite in later zoeal stages	Posterolateral spines on abdominal somite	Dorsal spine on abdominal somite	Telsonic spines in Stage I	No. of larval stages
Argis crassa	+	5	1	5	—	8 + 8	[1]2 or 3
A. dentata	+	5	1	5	—	8 + 8	3
A. lar	+	5	—	5	—	7 + 7	[1]3
Crangon alaskensis	+	—	1	5	3	7 + 7	5
C. communis	+	[2]1	1	5	—	7 + 7	[1]5
C. dalli	+	[2]5	1	5	—	7 + 7	5
C. franciscorum angustimana	+	[2]4	1, 2	5	3	7 + 7	[1]5
C. septemspinosa	+	—	1	5	3	7 + 7	5-6
Mesocrangon intermedia	+	[2]5	1	5	—	8 + 8	5
Paracrangon echinata	+	?	1, 2	1-5	1-5	?	7 +
Sabinea septemcarinata	+	?	1	5	—	16 + 16	[1]4
Sclerocrangon boreas	—	5	—	—	—	12 + 12	2
S. salebrosa	+	5	—	5	—	22 + 22	1
S. zenkevitchi	—	5	—	—	—	—	[1]2

[1]Estimated.
[2]Undeveloped pereopods.

crangon lar?, young stage" by Stephensen (1916); figure 3 in Stephensen (1916).

In Stage I, antennal scale with distal spine on outer margin; endopodite of maxillule and scaphognathite of maxilla with 6 setae each; abdominal somites 3-5 fringed dorsally with small spinules (spinules not mentioned for Atlantic specimens); telson and abdominal somite 6 jointed; telson with 8 + 8 setae. In megalopa, short, pointed rostrum extends to middle of eye; carapace with 2 dorsal teeth, ventral edge fringed with short plumose setae; abdominal somite 5 without posterolateral spines. Length: Stages I-III, 8.0-12.0 mm. Range: Sea of Japan to Anadyr Gulf, Gulf of Georgia, and San Juan Islands, WA; arctic Canada to Nova Scotia, Canada; depth, intertidal to 2,090 m (Butler 1980).

Argis lar (Owen)

Probably 3 larval stages.
Stages I and II, from plankton; described as *Nectocrangon lar* by Makarov (1967); figure 22 in Makarov (1967).
Not Crangonidae "Species F" (described by Kurata 1964b), as assumed by Makarov (1967).[10]

In Stage I, telson and abdominal somite 6 not jointed; telson with 7 + 7 setae. In Stage II, telson with 8 + 8 setae. Abdominal somites without spinules. Length: Stages I and II, 6.2-7.5 mm. Range: Sea of Japan to Chukchi Sea to Strait of Georgia, WA; depth, 10-280 m (Butler 1980).

Genus *Crangon* Fabricius (= *Crago* Lamarck)

Five or six zoeal stages. Anteroventral margin of carapace denticulate in most if not all larval stages. In all described stages, rostrum about 1/3 carapace length, spiniform, without teeth; posterolateral spines on abdominal somite 5; exopodites develop on either pereopod 1 or pereopods 1 and 2; abdominal somite 3 usually with dorsal spine; telson always widens posteriorly, with setae and $\leq 8 + 8$ spines.

Crangon alaskensis Lockington

Five larval stages.
Stages I-VII (Stage VI, first juvenile), known parentage; illustrations 1-79 in Loveland (1968).

In all described stages, rostrum barely reaches beyond eyes; dorsal spine on abdominal somite 3. Length: Stages I-V, 2.0-3.3 mm. Range: Kuril Islands; Bering Sea to Puget Sound, WA; depth, intertidal to 275 m (Butler 1980).

Crangon communis Rathbun[11]

Only Stage I described, known parentage; described as *Sclerocrangon communis* by Ivanov (1968); figure 1 in Ivanov (1968).
Not Stages II-V *C. communis* from plankton; described by Makarov (1967) as *Sclerocrangon communis*.[12]

Antennal flagellum about 3/4 length of antennal scale; antennal scale with 14 setae; abdominal somites without keels; spinules on posterior margins of abdominal somites 3-5. Length: Stage I, 4.8 mm. Range: Sea of Japan to Chukchi Sea to San Diego, CA; depth, 16-1,537 m (Butler 1980).

Crangon dalli Rathbun

Five larval stages.
Stage I, known parentage; Stages II-V and VI (first juvenile, "postlarval"), from plankton; figure 18 in Makarov (1967). Larvae figured in part but not described. Larvae thought to be identical morphologically to *C. allmani* larvae from the Atlantic Ocean (Makarov 1967).
Stage I from plankton; figures 7-9 in Birshteyn (1938).
Not "last (?) stage" as described by Birshteyn (1938) (see Makarov 1967).

Typical unabbreviated crangonid development. In all described stages, carapace without dorsal, lateral, or supraorbital spines; anterior margin of carapace denticulate; rostrum spiniform, without teeth;

[10]Morphological differences are too great for Makarov's *Nectocrangon lar* larvae and Kurata's "Species F" larvae to be identical. Makarov's larvae lack exopodites on pereopods in all stages and, in Stages I and II, have posterolateral spines on abdominal somite 5. Kurata's "Species F" larvae, known only in Stage II, have an exopodite on pereopod 1 and posterolateral spines on abdominal somites 5 and 6.

[11]Zarenkov (1965) proposed placing *C. communis* in a new subgenus, *Neocrangon*. Butler (1980) has shown that Zarenkov's diagnosis for *Neocrangon* is invalid, at least for British Columbia species. Based on Butler's findings, I have retained *C. communis* in the genus *Crangon*.

[12]It is unlikely that Makarov's (1967) larvae and Ivanov's (1968) larvae are the same species because Makarov's larvae have keels on abdominal somites 2 and 3, whereas Ivanov's larvae do not.

posterolateral spines on abdominal somite 5; abdominal somites without spinules or keels; telson always widens posteriorly, never with > 1 pair of lateral spines. In Stage V, pleopods uniramous, with buds of endopodites. Length: Stages I-V, 2.8-7.0 mm. Range: Sea of Japan to Chukchi Sea, to Puget Sound, WA; depth, 3-630 m (Butler 1980).

***Crangon franciscorum angustimana* Rathbun**

Only Stage I described, known parentage; figure 1 in Haynes (1980b).

Rostrum extends beyond eyes; carapace without shallow transverse groove; antennal scale with 10 plumose setae including subterminal seta along outer margin; endopodite with 4 segments on maxilliped 1, and 5 segments on maxilliped 3; exopodites of maxillipeds not jointed; pereopods 1-4 present but undeveloped; buds of exopodites on perepods 1 and 2; median dorsal spine on abdominal somite 3; posterolateral spines on abdominal somite 5; fifth pair of telsonic spines about equal in length to fourth and fifth pairs. Length: Stage I, 2.8-3.3 mm. Range: Kachemak Bay, AK, to Tillamook Rock, OR; depth, 18-183 m (Butler 1980).

***Crangon septemspinosa* Say**

Described from specimens from both Atlantic and Pacific Oceans.
Five or six larval stages.
Stages I and II, known parentage; Stages III-VI, from plankton; described as *C. affinis* by Kurata (1964b); Pacific specimens; figures 1-29 in Kurata (1964b).
Stage I, known parentage; Stages II-V, from plankton; Atlantic specimens; described as *Crago septemspinosus* Say by Needler (1941); figures 1 and 2 in Needler (1941).
Stages I-X (Stage X, first juvenile stage), known parentage (larval series likely includes extra stages); Atlantic specimens; figures 1-51 in Tesmer and Broad (1964).
Stages I-V, from plankton; Pacific specimens; figure 20 in Makarov (1967).

Discrepancies among descriptions may result, at least in part, from geographical variations in morphology. The following synopsis is based on specimens from off Hokkaido, Japan (Kurata 1964b). In all described stages, shallow transverse groove in carapace; dorsal spine on abdominal somite 3, posterolateral spines on abdominal somite 5. Exopodite only on pereopod 1. In Stage I, antennal scale with 11 setae, including 2 subterminal setae along outer margin; endopodites of maxillipeds 1-3 with 4 segments; exopodites of maxillipeds jointed; fifth pair of telsonic spines distinctly shorter than fourth or sixth pairs. Length: Stages I-V, 1.9-5.0 mm. Range: Prince Edward Island, Canada (Needler 1941); Beaufort, NC (Tesmer and Broad 1964); an estuarine, subarctic boreal species, Sea of Okhotsk (Makarov 1967); Hokkaido, Japan (Kurata 1964b); depth, 0-90 m, rarely to 440 m (Holthuis 1980).

Genus *Mesocrangon* Zarenkov

Largest larvae of Crangonidae with unabbreviated development. From Stage III on, posterior margin of telson straight or slightly concave.

***Mesocrangon intermedia* (Stimpson)**

Five larval stages.
Stages I-V, from plankton; described as *Sclerocrangon intermedia* by Makarov (1967); figure 24 in Makarov (1967).

In Stage I, antennal flagellum about half as long as antennal scale; antennal scale with 11 setae; abdominal somites 2-3 with keels; abdomen apparently without spinules. Length: Stages I-V, 4.5-9.0 mm. Range: Sea of Okhotsk to St. Lawrence Island (Bering Sea); depth, 18-180 m (Makarov 1967).

Genus *Paracrangon* Dana

In all described stages, rostrum long, spiniform, spinulose, directed upwards about 45°; carapace with denticulate anteroventral margin; basipodite of maxilliped without subterminal seta; exopodites on pereopods 1 and 2; exopodites of pereopods 1 and 2 with ≤ 6 natatory setae; protopodite of antenna with 2 spines – one at base of flagellum, other a long spine at base of scale.

***Paracrangon echinata*[13] Dana**

At least 7 larval stages.

[13]A diagnostic character of adult *Paracrangon* is the absence of pereopods 2 (Rathbun 1904). Kurata's (1964b) description of *Paracrangon echinata* shows pereopod 2 fully developed as late as the seventh larval stage. Either Makarov's (1967) identification of these larvae as *P. echinata* is incorrect, or *P. echinata* must have at least 3 or 4 more larval stages before pereopod 2 becomes reduced or absent.

Stages II, IV-VII, from plankton; tentatively identified as *Glyphocrangon* sp. by Kurata (1964b); figures 103-130 in Kurata (1964b).

Stages II and IV; Makarov (1967) based identity on known distribution of adults and morphology of embryo of *Glyphocrangon granulosis* (see Bate 1888); figure 28 in Makarov (1967).

Most spinose of crangonid larvae known from northern North Pacific Ocean (Fig. 10). Length: Stage II, 5 mm; Stage VII, 13.8 mm. Range: Sea of Japan; Okhotsk Sea; Port Etches, AK, to La Jolla, CA; depth, 7-201 m (Butler 1980).

Genus *Sabinea* J. C. Ross

Probably 4 larval stages. In all described stages, telson relatively wide, with shallow indentation; pereopods 2-5 without exopodites.

Sabinea septemcarinata (Sabine)

Probably 4 larval stages.

Prezoeal telson and Stages I and III, probably known parentage; Atlantic specimens: plate V, figures 1-23, and plate VI, figures 1-13, in Sars (1890).

Stages I and III, probably known parentage; described as *Crangon septemcarinatus* by Williamson (1915); figures 167-172 in Williamson (1915). Williamson's figures from Sars (1890).

Stages I and III, from plankton; figure 12, "last stage" (= Stage III), in Birshteyn (1938).

Stage I (whole larva) and Stage III (telson); origin of specimens not given; figures 1 and 2 in Williamson (1960).

Stages and origin of specimens not given, described as *Myto gaimardi* by Birshteyn (1938); plate 7, figure 1 (Krøyer 1846 in Birshteyn 1938).

In all described stages, anteroventral margin of carapace with about 7 denticles. Abdominal somites 1-4 with 1, 2, 1, and 1 ventral spines, respectively; abdominal somite 5 with posterolateral spine. Telson with 16 + 16 setae in Stage I, 13 + 13 setae in Stage III. Length: Stages I-III, 7.7-11.5 mm. Range: area of Iceland and Faroe Islands (Williamson 1960); Barents and Norwegian Seas (Williamson 1960); Chukchi Sea (Birshteyn 1938); eastern coast of North America from mouth of St. Lawrence River to Massachusetts Bay; Arctic Ocean to Point Barrow (Alaska), White Sea, and northern Europe (Williams 1974); depth, 10-240 m (Williams 1974).

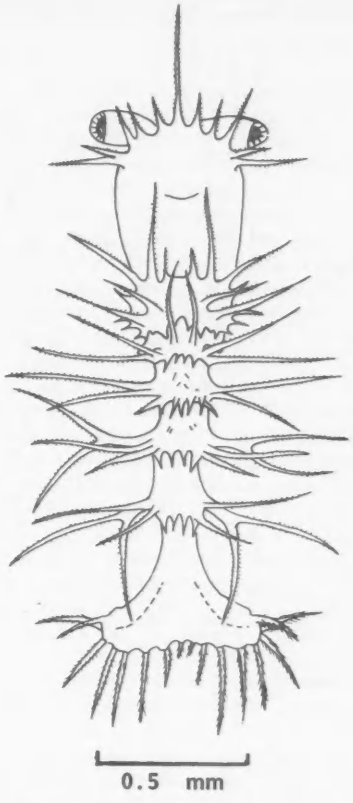

FIGURE 10.—Dorsal view of body, Stage I zoea of *Paracrangon echinata*.

Genus *Sclerocrangon* G. O. Sars

Not more than 2 larval stages. Appendages resemble adult except uropods enclosed and pleopods not fully setose. Pereopods without exopodites; pereopods 4 and 5 have characteristic sickle-shaped dactyli (Fig. 11).

Sclerocrangon boreas (Phipps)

Two larval stages.

Late embryo extracted from egg; plate VI, figures 14-28, in Sars (1890, as cited in Williamson 1960).

Stage not specified, known parentage (Makarov 1967). No figures.

Stage I and Stage II ("postlarval"), known parentage; figures 1-3 in Makarov (1968).

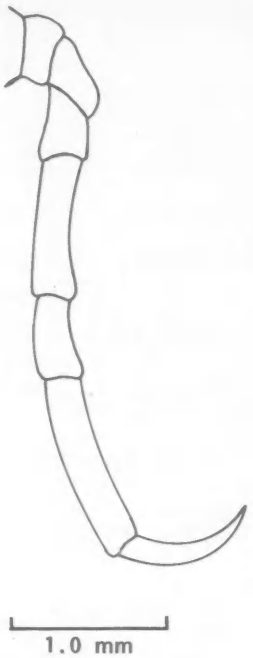

FIGURE 11.—Pereopod 4 or 5 of *Sclerocrangon* larva with characteristic sickle-shaped dactyl.

Larvae not free living but cling to pleopods of female. In all described stages, carapace without anteroventral denticles; flagellum of antennule segmented; basal portion of antennule shaped as in adult; maxillipeds with undeveloped exopodites; exopodites with a few feeble natatory setae; pereopods segmented, without exopodites. In Stage I, rostrum absent; carapace covers sessile eyes; telson and abdominal somite 6 jointed. In Stage II, rostrum short, triangular, flattened dorsoventrally. Length: Stage I, 9.0 mm; Stage II, 11.5 mm. Range: Sea of Japan to Chukchi Sea to Bare Island, WA; arctic Canada to Cape Cod, MA; North Atlantic Ocean and arctic Europe; Spitsbergen to Faroe Islands; depth, 0-366 m (Butler 1980).

***Sclerocrangon salebrosa* (Owen)**

One larval stage.

Stage I, from plankton; figure 27 in Makarov (1967).

Embryos, from female; Stage I and Stage II ("post-larval"), from plankton; figures 1 and 2 in Makarov (1968). Larvae from plankton identified by comparison with embryos dissected from eggs.

Larvae free living. In Stage I, rostrum spiniform; carapace with anteroventral denticles; exopodites of maxillipeds fully developed, each exopodite with 5 natatory setae; telson exceptionally wide with 22 + 22 setae. Length: Stage I, 10.3-10.5 mm. Range: Okhotsk Sea; Hokkaido; no depth range (Kurata 1964b; Makarov 1967).

***Sclerocrangon zenkevitchi* Birstein and Vinogradov**

Only Stage I described, known parentage; figure 5 in Birshteyn and Vinogradov (1953).

Carapace nearly circular laterally, without rostrum; cephalothorax and abdomen without spines or denticles; telson ovoid. Length: Stage I, 7.2 mm. Range: Bering Sea; depth, 2,995-3,940 m (Birshteyn and Vinogradov 1953).

BIOLOGY

Although pandalid, hippolytid, and crangonid larvae are common inhabitants of the neritic meroplankton of temperate and arctic waters of the North Pacific Ocean, only a few studies on their biology have been published. The most complete studies are those of Haynes (1983), Makarov (1967), and Rothlisberg (1975). Haynes described the relative abundance and distribution of pandalid shrimp larvae in the lower Cook Inlet-Kachemak Bay area, Alaska; Makarov (1967) described the distribution of decapod shrimp larvae of the West Kamchatkan shelf; and Rothlisberg (1975) discussed larval ecology of *Pandalus jordani* off the Oregon coast. In this section, I review the findings of these authors and supplement their findings with information from the literature. To avoid redundancy of citation, only information in addition to that given by Haynes, Makarov, and Rothlisberg is cited by author and date. This section does not include every known facet of the biology of decapod shrimp larvae of the northern North Pacific Ocean; however, more information can be acquired from the papers of Haynes, Makarov, and Rothlisberg and from their bibliographies.

Areas of high abundance of Stage I larvae apparently indicate areas where females are releasing larvae. For example, in Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis*, *P. goniurus*, *P. hypsinotus*, and *Pandalopsis dispar* were most abundant in plankton samples collected in the same area

where females were releasing larvae (for these 4 species, females were releasing larvae at depths of about 85, 35, 50, and 100 m, respectively, based on a trawling survey).

Time of release of pandalid larvae varies with species. In Kachemak Bay in 1972, Stage I larvae of *Pandalus borealis* were not caught until the first half of April; Stage I larvae of *P. goniurus* and *P. hypsinotus* were caught later, in the latter half of April. In British Columbia waters, *P. borealis* larvae are also released earlier than larvae of either *P. goniurus* or *P. hypsinotus* (Berkeley 1930; Butler 1964).

Time of larval release is also related to water temperature. For example, a residual layer of relatively cold (sometimes subzero) water remains on the central West Kamchatkan shelf at a depth of 50-150 m throughout the summer. Decapods living in this layer of cold water release their larvae later than decapods living in warmer waters to the north and south. In the western North Atlantic Ocean, pandalid shrimp also release their larvae later in colder waters than in warmer waters (Haynes and Wigley 1969).

Depth distributions of larvae of *P. borealis* and *P. goniurus* in Kachemak Bay, 1972, were usually similar. Few larvae were in the 0-10 m stratum; most were between about 10 and 40 m. The abundance of larvae remained relatively constant below about 50 m. Numbers of Stage I *P. borealis* larvae, however, increased below about 70 m, possibly reflecting their recent release. These depth distributions differ from the depth distribution of *P. jordani* off the Oregon coast. Younger (Stages V-X) *P. jordani* larvae were found closer to the surface (0-10 m stratum) than older (Stages XI-XV) larvae (to 160 m).

Water temperature has profound effects on larval survival, growth, and size at metamorphosis. For example, survival of *P. jordani* larvae (Stages I-III) is markedly less at 17° than at 5°C. For the oldest stage (Stages IX-XIII), the relation between survival and temperature is reversed, and survival is lowest at 5°C (Rothlisberg 1979). For larvae of *P. platyceros*, survival is reduced by sudden changes in temperature, particularly about 20°C and below 9°C (Wickins 1972). At a given temperature (range 5°-14°C), growth increments for all larval stages of *P. jordani* decrease with increasing size; however, the higher the temperature, the more rapid the molting frequency (Rothlisberg 1979).

Shrimp larvae can probably influence the direction and extent of their dispersal. For instance, in Kachemak Bay, 1972 and 1976, pandalid shrimp larvae were released in the central portion of the outer bay. Some of these larvae were carried northward out of the bay in the direction of the current, but others were dispersed southwestward in a direction opposite the current. In the southern area of the western Kamchatka shelf, *Crangon* larvae released close to shore with larvae of other species, such as king crab, *Paralithodes camtschatica*, remained close to shore. Larvae of the other species, however, were carried seaward. In the northern area of the western Kamchatka shelf, where currents are faster than in the southern area, *Crangon* larvae were carried seaward (Makarov 1967). The causes for dispersal of larvae against known water currents are unknown, but dispersal may be dependent, at least in part, on the swimming capability of the larvae.

Some pandalid shrimp larvae migrate vertically in a diel cycle. In Kachemak Bay in 1972, Stages I and II larvae of *P. borealis* and *P. goniurus* were most abundant between the surface and 15 m during low light levels (1800-0800 h); however, during high light levels (1000 and 1600 h), they were most abundant between 30 and 60 m. Although present, a pronounced thermocline did not prevent larvae from moving vertically. Whether later stages of *P. borealis* and *P. goniurus* migrate similarly is unknown; however, in waters off Oregon, only Stages XII-XVI larvae of *P. jordani* migrate vertically in a diel cycle. During the day, these *P. jordani* larvae are distributed from the surface to 150 m by age: the deeper the water, the older the larvae. At night, *P. jordani* larvae migrate upwards in the water column, and the stages remain somewhat uniformly distributed with depth.

Foods of pandalid larvae have been determined during attempts to rear the larvae in the laboratory and from examination of shrimp stomachs. Larvae of *P. jordani* and *P. platyceros* have been reared on brine shrimp, *Artemia salina* nauplii (Modin and Cox 1967; Lee 1969; Price and Chew 1972), *P. hypsinotus* larvae have been reared on brine shrimp nauplii and algae (Haynes 1976), and *P. kessleri* larvae have been reared on small pieces of crab, shrimp, and mussel tissue (Kurata 1955). In 1976, I made a preliminary study (unpublished) on foods eaten by pandalid shrimp larvae in Kachemak Bay by examining their gut contents. The larvae mostly ate diatoms, especially *Coscinodiscus* types, and larval crustaceans. Many of the guts also contained black pigment and ommatidia. The assumption that pandalid larvae feed on eyes of other decapod larvae was subsequently confirmed when I observed a *P. borealis* zoea ingesting the eye of a live king crab zoea. Calcareous fragments (probably molluscs), coccolithophores, spines of larval echinoderms, and

bits of diatoms have been found in guts of *Pandalus* larvae from European waters (Lebour 1922).

Some species of pandalid larvae are sustained by their internal yolk for several days after hatching without feeding; others must feed immediately after hatching or die. *Pandalus platyceros* larvae can live 11-13 d on stored yolk with no food (Price and Chew 1972); however, when food is offered, they feed immediately after hatching. In Price and Chew's (1972) study, the starved larvae ate their dead relatives, but did not actively prey on them. Larvae of *P. jordani*, however, if not fed soon after hatching, starve and die regardless of later increases in prey concentrations (Modin and Cox 1967). In another study, 40% of Stage I zoeae of *P. borealis* without prey died in 5 d, and 100% died in 13 d (Paul et al. 1979).

The relationship between food and survival in captivity has been determined for some North Pacific Ocean larvae; however, little is known about this relationship in nature. For instance, year-class strength may be influenced or even largely determined by the quality and quantity of food available during the larval period. Unfortunately, there is virtually no information on the types and quantities of food needed for survival of shrimp larvae in nature. Until this information is available, the relation between food and survival of shrimp larvae at sea will remain unknown.

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WITHIN-SEASON DIFFERENCES IN GROWTH OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS HARENGUS*

CYNTHIA JONES[1]

ABSTRACT

Data obtained from two previous studies of larval Atlantic herring growth were compared, based on otolith increment estimated age. These data, from the Gulf of Maine in 1976-77 and 1978-79, supported the hypothesis that larvae hatched early in the spawning season grew faster than larvae hatched late. Differences were significant under assumptions that increments were deposited in the otolith either daily or at 0.5 increments per day. Corroborative evidence indicated that otolith increments were formed daily at least during the early part of the spawning season.

The otolith increment technique has been used to estimate age and growth in field-caught larval Atlantic herring, *Clupea harengus harengus*, in the Gulf of Maine by Townsend and Graham (1981) and by Lough et al. (1982). Use of the increment technique to estimate age usually assumes daily deposition of otolith increments. Uncertainty exists, however, regarding increment deposition rates in the otoliths of larval herring. Gjosaeter (1981) and Øiestad (1982) have observed daily increment deposition. In contrast, Geffen (1982) found that increment deposition can be variable and a function of growth rate in larval herring, underscoring the problem in simply assuming that increments occur daily under field conditions. Growth calculations based on assumptions of daily increment deposition in populations that experience variable increment deposition rate would result in inaccurate estimates of growth rates. In most cases where otolith increment deposition has been tested under suboptimal conditions, the deposition rate has been found to be nondaily (for review see Jones 1984). Estimates of growth rates can be made, however, by expressing growth based on increment counts and with the use of corroborative evidence to determine periodicity of increment deposition.

Das (1968) found that growth rates of larval Atlantic herring, measured by following the progression of length modes over time, were different within a spawning season. He stated that early-spawned larvae grew faster than late-spawned larvae and modeled growth with curvilinear functions. Townsend and Graham (1981) also reported two different growth rates for Atlantic herring, one for larvae born prior to November 5 and one for larvae born later. Each group was modeled by two regression lines to emphasize that growth ceased in January and resumed in February. In their study, early- and late-hatched groups were analyzed separately and the comparison of growth between larvae hatched early versus late in the season was not statistically verified.

This paper uses otolith increment data from Townsend and Graham (1981) and from Lough et al. (1982) to compare early-season versus late-season larval Atlantic herring growth. The comparisons are made using the assumptions of both daily and nondaily otolith increment deposition.

METHODS

Raw data for otolith counts and larval fish lengths used in these studies were obtained from Gregory Lough of the National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA, and from Joseph Graham and David Townsend of the Maine Department of Marine Resources, Boothbay Harbor, ME. Both data sets were used in the detection of within-season differences in growth rates. Although the study of Lough et al. (1982) encompassed a larger area, only data from the Gulf of Maine were included in the analysis (Table 1), in order that comparisons were made within the same area as for Townsend and Graham (1981). Methods employed for the collection of data were reported by Lough et al. (1982) and by Lough and Bolz (1979) for the 1976-77 data and by Townsend and Graham (1981) for the 1978-79 data.

For each season (1976-77, 1978-79), data were analyzed in three ways:

[1]Graduate School of Oceanography, University of Rhode Island, Kingston, RI 02882-1197; present address: Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY 14853.

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TABLE 1.—Station information for Atlantic herring samples from the Gulf of Maine area for the fall and winter of 1976-77 sampling program. (Data from Lough et al. 1982.)

Vessel	Cruise No.	Stn.	Lat. N	Long. W	Date	Time (Night or Day)
Annandale	76-01	38	43°37′	69°22′	8 Oct.	0300 (N)
		44	43°44′	68°50′	8 Oct.	1415 (D)
		59	44°25′	67°35′	9 Oct.	1515 (D)
		65	44°36′	67°07′	13 Oct.	0330 (N)
Researcher	76-01	102	42°58′	70°00′	8 Dec.	1030 (N)
		105	43°30′	69°30′	9 Dec.	1100 (N)
Mt. Mitchell	77-01	122	43°14′	70°01′	24 Feb.	1620 (D)
		123	43°00′	70°15′	24 Feb.	1933 (D)

1) Hatch date was calculated on the assumption of daily increment deposition, and all data were considered.
2) Hatch date was calculated on the assumption of daily increment deposition only with larvae which had 60 or fewer increments included for analysis. This was done to determine whether growth differences were present in the earlier months of life. Also, since the range of increment counts for the late-hatched larvae from 1976 to 1977 was greater than for early-hatched larvae, use of a truncated data set resulted in more valid comparisons.
3) Hatch date was calculated on the assumption of nondaily deposition (0.5 increment/d).

Date of hatching was calculated by subtracting the estimated age of each larva from its date of capture. This calculation, of course, depends on how age was estimated. According to the Lough et al. (1982) calculation, a larva with 10 otolith increments would be 29 d old: 22 d for the first 3 increments, plus 7 d to lay down the next 7 increments. According to the assumptions used by Townsend and Graham (1981), a larva with 10 otolith increments would be 15 d old, assuming that increment deposition began 5 d after hatch, and was daily thereafter. There is a difference of 14 d between these two estimates of age, and, therefore, estimated day of hatch. This does not affect the regression analysis, as long as the independent variable used is increment count, not age.

The range of possible hatch dates for each individual was also calculated, based on the consideration that deposition rates could vary from 0.5 to 1.0 increment/d (after Geffen 1982). Age could be equal to the number of increments plus a constant (5 d) or up to twice the number of increments plus a constant (5 d).

Larvae were classified as either early- or late-hatched within the spawning season. For 1976-77 the early-late division date was placed at the discontinuity in the frequency of hatching plot, which also occurred at the midpoint in the spawning cycle. Division date for the 1978-79 data set was placed at approximately the division of Townsend and Graham (1981) which they felt represented two different groups of larvae.

For analysis of nondaily deposition, the data were partitioned to insure that there could be no overlap of early- and late-hatched classification of larvae, assuming deposition ranged from daily deposition to deposition of one increment every 2 d. Any late-hatched larva whose possible range of hatch dates overlapped the division date (for early-hatched vs. late-hatched classification) was eliminated from analysis. This resulted in a loss of data (e.g., the fish whose possible hatch date overlapped the division date) and decreased the ability to detect differences.

Ordinary least squares linear regressions were fit to each data set. Bartlett's test for homogeneity of variance (Ostle and Mensing 1975) was applied to the data before each analysis. After regressions were fit, the residuals of length were plotted against predicted length and examined for trends (Draper and Smith 1981). F-tests (Ostle and Mensing 1975) were applied to paired linear regressions, early-hatched versus late-hatched, to determine whether the slopes were significantly different. This test showed whether the data were better fit by two lines, one for early-hatched and one for late-hatched larvae, or whether a single regression line was preferable. In the regression plots the change in length is expressed in millimeters per increment.

The von Bertalanffy growth equation,

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

was also fitted to the data, using the nonlinear regression procedure (NLIN) within SAS (Statistical Analysis Systems, SAS Institute, Cary, NC). Estimates of the parameters (K, L_∞, t_0) of the von Bertalanffy equations for early- and late-hatched larvae were compared with a Fisher-Behrens test (Hoenig 1982) to determine whether the vector of parameter estimates from the two classifications was significantly different.

RESULTS

Linear regression models fitted to larval length-at-increment count data showed significant differences between larvae hatched early and late in the spawning season. Larvae hatched early had achieved greater length at a given increment count than those

hatched later. Intercepts were not compared since the data sets did not contain any larvae with fewer than seven increments and inferences outside the range of the data should not be drawn.

1976-77 Study

A frequency plot of hatching dates for the Gulf of Maine stations is shown in Figure 1 for age estimated on the assumption of daily ring deposition and in Figure 2 for age estimated on the assumption that deposition was daily or as little as one ring every other day.

Differences in length-at-increment count between early- and late-hatched larvae was striking (Table 2). Regression plots are shown in Figure 3. Analysis of the data confirmed that the length-at-count data were modeled more accurately by two different regression lines ($P < 0.01$) and that the slopes of these two regressions were significantly different (P

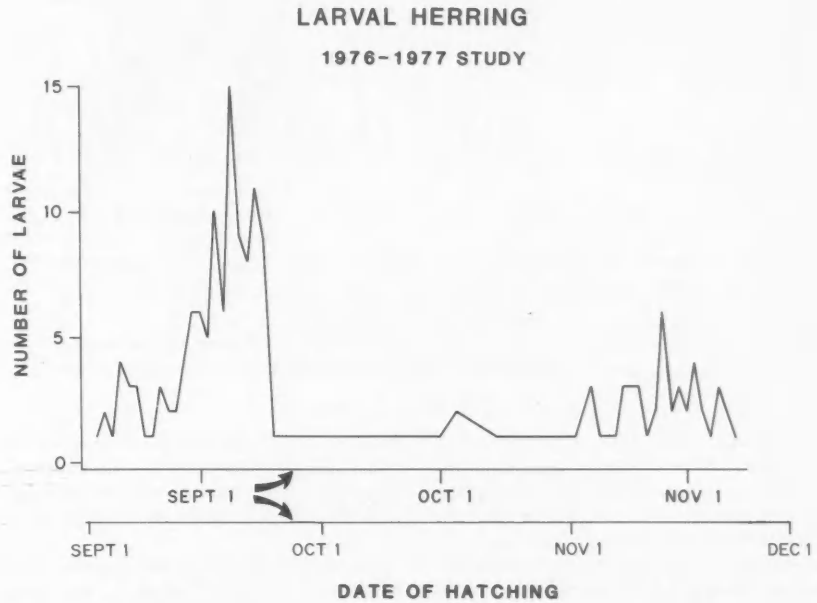

FIGURE 1.—Frequency of Atlantic herring hatching during the 1976-77 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method, or, as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

TABLE 2.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	64	15.8	0.0948	0.0047	0.87		
60 or fewer	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	44	14.6	0.1470	0.0274	0.41		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early versus late for each group.

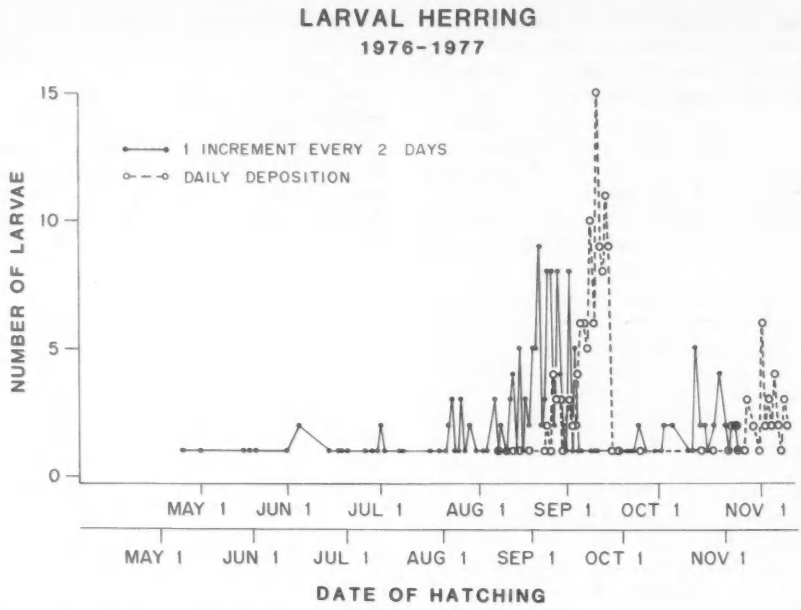

FIGURE 2.—Frequency of Atlantic herring hatching during the 1976-77 study, calculated under two assumptions of otolith increment count and age relationship.

< 0.01). The average length achieved per increment was 0.33 mm and 0.10 mm for early- and late-hatched larvae, respectively. Bartlett's test confirmed that variances were homogeneous. Analysis of residuals showed that the last three residuals, corresponding to the three largest larvae, were below the average. The exclusion of these points did not alter the results of the analysis.

Analysis of the subset of larvae with fewer than 60 increments (Table 2) showed that data were better fitted with two different regression lines ($P < 0.01$) and that the slopes were significantly different ($P < 0.01$). Regression plots are shown in Figure 4. Change in length of early-hatched larvae was 0.33 mm/increment and 0.15 mm/increment for late-hatched larvae. Bartlett's test showed variances to be homogeneous and residuals showed no trends, except for the two youngest late-hatched larvae which fell below the regression line. Late-hatched larvae were slightly larger than early-hatched larvae for the lowest increment counts.

Differences in length-at-increment count were apparent for data whose calculated hatch dates included deposition rates of from 0.5 to 1.0 increments/d (Table 3). The change in length of early-hatched larvae was 0.33 mm/increment compared with 0.17 mm/increment for late-hatched larvae. Data were again better fit with two regression lines ($P < 0.01$) whose slopes were significantly different ($P < 0.01$).

The von Bertalanffy growth equation fit the late-hatch larval data well (Table 4). L_∞ was estimated at 29.81 mm, with a 95% confidence interval of 26.41 to 33.22 mm. Fit to the early-hatched larval data was poor. L_∞ was estimated at 35.59 mm, with a confidence interval of 17.76 to 53.41 mm. These data were adequately fit with a straight line, and there is little justification for fitting with a curvilinear function other than it has been traditionally used for adult fish. Beverton and Holt (1954), however, stated that the von Bertalanffy equation should not necessarily be used during the early life stages. Nevertheless, when the parameter estimates from the two curves were compared, they were signifi-

FIGURE 4.—Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Lough et al. (1982).

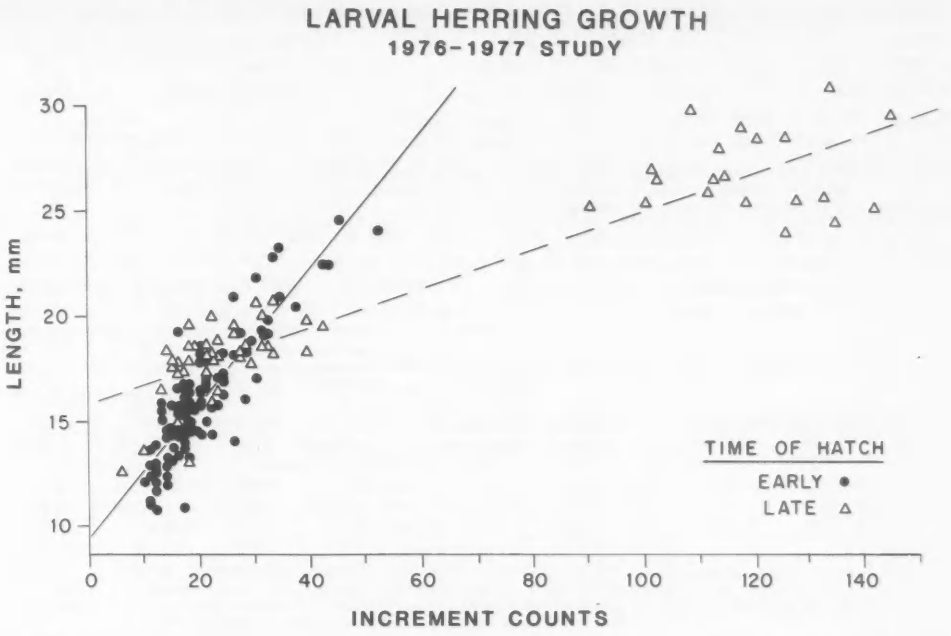

FIGURE 3. – Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Lough et al. (1982).

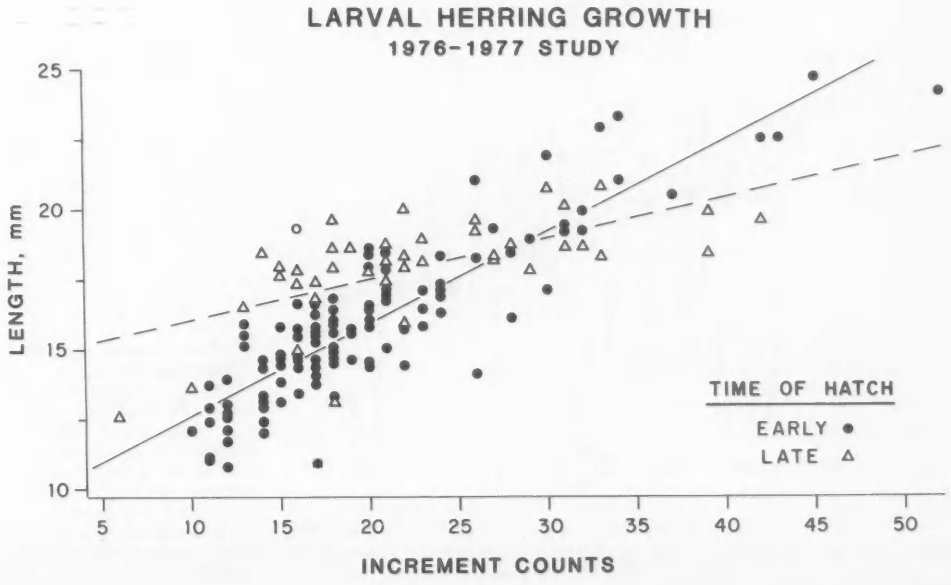

TABLE 3.—Regression analysis of 1976-77 Gulf of Maine Atlantic herring data based on two otolith increment deposition assumptions. (Data from Lough et al. 1982.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	117	9.4	0.3284	0.0172	0.76	<0.01	<0.01
	Late	39	14.2	0.1711	0.0364	0.37		

Legend: Data were classified into early- and late-hatched larvae. Two dates of hatch were calculated: 1) Age equalled increment count plus a constant, and 2) age equalled twice the increment count plus a constant. This resulted in a range of potential hatching dates. Any late-hatched larva whose range of hatch date overlapped the division date (Text Fig. 1) was eliminated from the analysis.

TABLE 4.—Estimation of von Bertalanffy growth parameters for larval Atlantic herring from the Gulf of Maine.

Year	Hatch classification	Parameter	Estimate of parameter	Standard error of estimate	95% confidence interval Low	95% confidence interval High
1976-77	Early	K	0.01865	0.00939	0.00008	0.03723
		L_∞	35.6	9.0	17.8	53.4
		t_0	−12.3	5.00	−22.2	−2.41
	Late	K	0.01530	0.00457	0.00616	0.02443
		L_∞	29.8	1.7	26.4	33.2
		t_0	−38.01	12.46	−69.92	−13.10
1978-79	Early	K	0.00262	0.00158	−0.00050	0.00575
		L_∞	113.2	48.8	16.3	210.1
		t_0	−42.28	9.94	−62.00	−22.57
	Late (convergence criteria could not be met)					

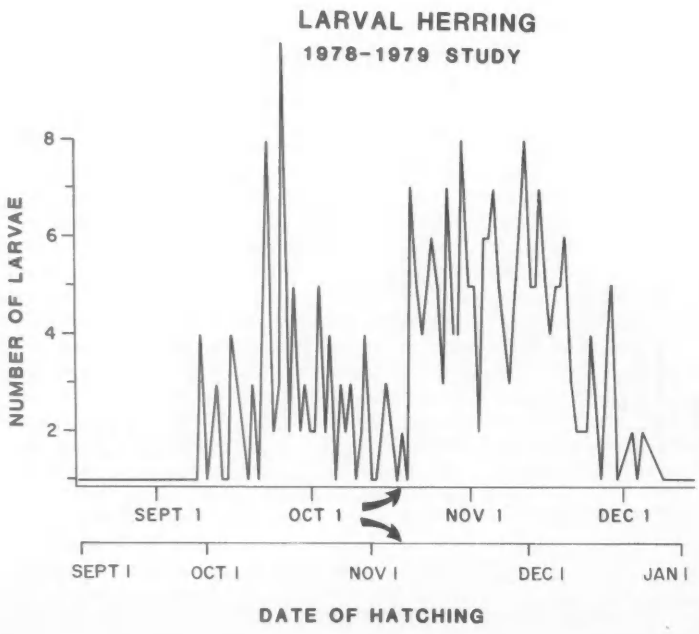

FIGURE 5.—Frequency of Atlantic herring hatching during the 1978-79 study. Upper scale gives the day of hatch based on the Lough et al. (1982) aging method as discussed in the text. Lower scale gives the day of hatch based on Townsend and Graham's (1981) aging method as discussed in the text. Arrow indicates division point between early- and late-hatched classification.

cantly different ($P < 0.01$)—early-hatched larvae grew faster than late-hatched larvae.

1978-79 Study

A frequency plot of hatching dates under the assumption of daily increment deposition for larvae sampled in the Sheepscot estuary is shown in Figure 5.

Analysis (Table 5) showed that the data were better fit with two lines ($P < 0.01$) and that the slopes were different ($P < 0.01$). The change in length was 0.21 mm/increment and 0.18 mm/increment for early- and late-hatched larvae, respectively (Fig. 6). However, the results should be interpreted with the knowledge that Bartlett's test showed the variances to be heterogeneous. This could have been caused by actual heterogeneity of variances, or by nonnormality in the data. The F tests used in these analyses assumed equal variances between the hatch classifications. Cochran (1947) reported, however, that lack of homogeneity would decrease the power of an F test to discern true differences when they did, in fact, occur. Since differences were statistically significant, not meeting this assumption did not hinder analysis (the use of various transformations

TABLE 5.—Regression analysis of 1978-79 Gulf of Maine Atlantic herring data. (Data from Townsend and Graham 1981.)

Otolith increment count	Hatch classification	Sample size	Intercept	Slope of regression line	Standard error of slope	R^2	Probability intercepts equal	Probability slopes equal
All data	Early	102	13.3	0.2134	0.0661	0.92	<0.01	<0.01
	Late	198	14.2	0.1793	0.0060	0.82		
60 or fewer	Early	42	9.4	0.3378	0.0189	0.89	<0.01	<0.01
	Late	53	11.4	0.2434	0.0203	0.74		

Data were classified into early- and late-hatched larvae. These two groups were compared by fitting ordinary least squares regression lines to 1) all the data within the two classifications, and 2) using only lengths from larvae with 60 or fewer increment counts. Slopes and intercepts were compared between early vs. late for each group.

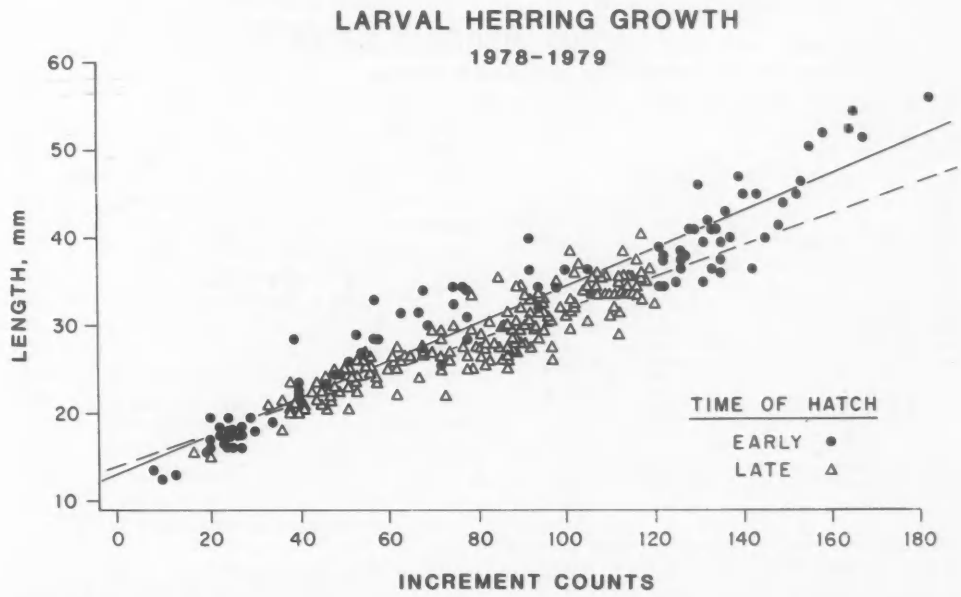

FIGURE 6.—Regression plot of length-at-otolith increment count for Atlantic herring. Complete data set represented. Data from Townsend and Graham (1981).

did not result in homogeneity of variances). Except for the residuals for three small larvae, analysis for residuals showed no trends.

For larvae with 60 increments and fewer (Fig. 7), Bartlett's test showed homogeneity of variance. These data were better fitted by two lines ($P < 0.01$); the slopes were significantly different ($P < 0.01$). The change in length was 0.34 mm/increment and 0.24 mm/increment for early- and late-hatched larvae, respectively.

The von Bertalanffy growth equation fit the early-hatched larval data poorly (Table 4). L_∞ was estimated at 113.22 mm, with a 95% confidence interval of 16.37 to 210.06 mm. The von Bertalanffy growth function could not be fitted (solution would not converge) to the late-hatched larval data.

The 1978-79 data could not be tested under assumptions that increment deposition could vary from 0.5 to 1.0 increment/d. Almost all of the calculated hatch dates for late-hatched larvae, estimated on deposition rates of 0.5 increment/d, overlapped the classification division date. Too few points were left for analysis.

DISCUSSION

Evidence from the Gulf of Maine supports the hypothesis that increase in length for herring larvae hatched early in the spawning season is greater than for larvae hatched late in the season. These differences were evident both under assumptions of daily otolith increment deposition and for deposition of one increment every other day. Before these differences are assumed to be due to differences in growth, however, there are other hypotheses which should be considered that could explain these observations. Differences could be the result of within-season changes in otolith increment deposition rates, or of differential mortality due to selective predation.

If there are within-season changes in otolith increment deposition rates, growth (change in length at age) could actually be similar, but the calculated growth rates would appear to be different because they are expressed as change in length per increment count. In order for this hypothesis to explain the above results, larvae born early in the season would be required to put down fewer increments per time period than would larvae born late in the season. The data allow a test of the hypothesis that larvae lay down fewer than 1 increment/d during the early part of the year. When estimated hatching dates are calculated for larvae caught early in the season, under the assumption that one increment was deposited every other day, some of these larvae

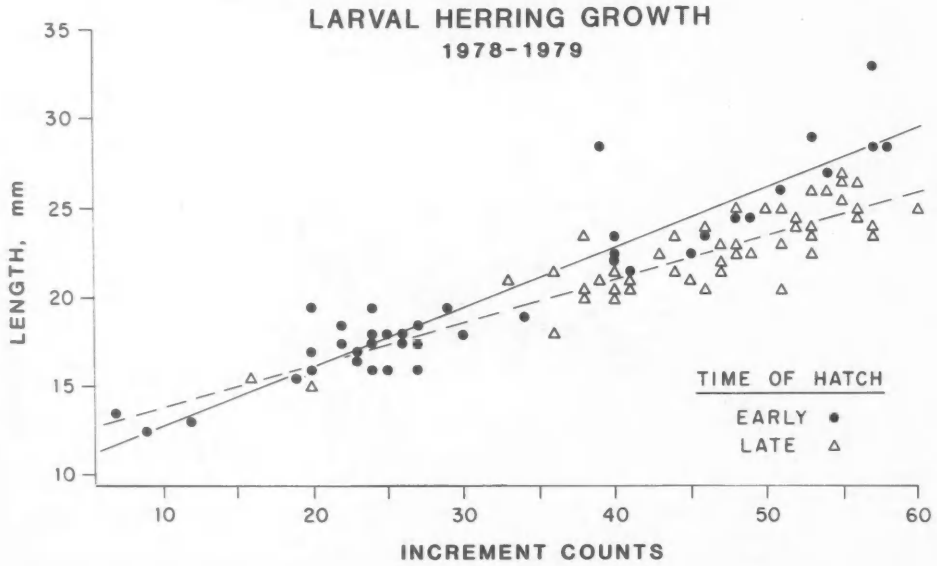

FIGURE 7.–Regression plot of length-at-otolith increment count for Atlantic herring. Only lengths for larvae with 60 or fewer otolith increments have been included for analysis. Data from Townsend and Graham (1981).

would have had to appear in the plankton in the middle of the summer (Fig. 3). However, newly hatched larvae are not found in significant numbers in the plankton before September (Boyar et al. 1973; Colton et al. 1979). It is far more plausible that larvae hatched early in the season, when growing conditions are more nearly optimal (Sherman and Honey 1971; Cohen and Lough 1983), deposit increments with close to daily periodicity. Hence, in order for this hypothesis to be true, late-hatched larvae would have to deposit increments at a rate greater than 1 increment/d. There is no evidence in the literature to support this for larval herring.

Difference in population growth rates within a spawning season could also result from a shift in size-specific mortality during the season. The observed differences in growth rate could result if early-hatched larvae have higher cumulative mortalities for slower growing individuals, while late-hatched larvae have higher mortalities for faster growing individuals. Progressively, fewer and fewer of the selectively predated larvae would be seen in older ages. This would result in differences in population growth rates that are not apparent for individuals within the population.

Although differential mortality cannot be dismissed with the available data, the most plausible explanation for the differences in length-at-increment count is an actual difference in larval growth rate over the spawning season. Such differences in population growth rate can be important for larval herring survival. Since greater time spent in the larval stage is thought to be related to increased mortality, it is interesting to note that an early-hatched larva from the 1978 study would require, on the average, 80 d to reach 30 mm, compared with 88 d for a late-hatched larva. For the 1976 study, it would take, on the average 63 d for an early-hatched larva to reach 30 mm compared with 157 d for a late-hatched larva to reach this size.

It has been shown that in both years, late-hatched larvae are larger than early-hatched larvae at the time of first increment formation. This could result from larger eggs being produced in the winter (Cushing 1967), or from different growth rates from hatch to the age of larvae covered in this study. Without further evidence of differences in egg size or actual growth rates between hatch and the age these studies began, neither hypothesis can be supported.

Differences in growth rate within the spawning season can contribute to error when using an age-length key to age larvae. For a given length, samples containing early-hatched larvae would yield different ages than samples containing late-hatched larvae. For the 1978-79 study (under the assumption of daily increment deposition), a 25 mm larva would average 60 increments for early-hatched larvae versus 56 for late-hatched larvae. For the 1976-77 study a larva of this length would average 47 versus 102 increments, respectively. This additional variation should be taken into consideration when using age-length keys for larvae.

Differences in growth during the spawning season might be due to changes in the environment when a species of fish spawns over a protracted time period, such as Atlantic herring which spawns from late August through November (Boyar et al. 1973; Colton et al. 1979). Early in the season copepods, the main food for larval herring (Sherman and Honey 1971; Cohen and Lough 1983), are more abundant than late in the spawning season (Sherman et al. 1983). Temperatures average 12°-16°C early in the season and < 8°C later in the season (Colton 1968; Colton and Stoddard 1972). Day length and metabolic demand may also vary over the spawning season. Alternately, differences in growth between larvae hatched early and late in the season could be the result of genetic differences if early and late spawners are from different stocks.

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SEASONAL CYCLES OF FAT AND GONAD VOLUME IN FIVE SPECIES OF NORTHERN CALIFORNIA ROCKFISH (SCORPAENIDAE: *SEBASTES*)

PATRICK J. GUILLEMOT,[1] RALPH J. LARSON,[2] AND WILLIAM H. LENARZ[3]

ABSTRACT

Seasonal changes in visceral fat volume and gonad volume are compared in five species of rockfish from northern and central California: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. In these species, visceral fat was deposited between spring and fall, at the same time as gametogenesis. Visceral fat declined in volume between fall and spring, coinciding with the decline in volume of testes and preceding the release of embryos in females. We suggest that increased feeding during the summer upwelling season provides the energy for simultaneous fat accumulation, gametogenesis, and perhaps somatic growth. During subsequent seasons of presumed food storage, these rockfishes may utilize visceral fat reserves for maintenance. This pattern of fat deposition and utilization may contribute to the long life and repeated reproduction of rockfishes, at the expense of current fecundity and growth.

Our data also suggest that rockfishes which spawn only once during the reproductive season have fat cycles of greater magnitude than those spawning more than once a year. Of the species that we studied, the apparent single spawners *S. entomelas* and *S. flavidus* have more northerly geographic distributions and larger fat cycles than the multiple spawners *S. goodei* and *S. paucispinis*. It is possible that the shorter and more pronounced productive season in the north leads to a greater need for fat reserves during winter and makes the wintertime production of additional batches of eggs energetically difficult.

The seasonal storage and utilization of lipid (and nonlipid) reserves are important in the metabolic activities and overall life histories of many animals (Love 1970; Shul'man 1974; Derickson 1976a and associated papers). While cycles of lipid storage and utilization are generally associated with seasonal changes in food availability (Derickson 1976b) or metabolic demands (Lawrence 1976), the functions of lipid storage are varied.

In many fishes, reserves are used primarily in reproduction, as indicated by complementary cycles of lipid content and reproductive activity (Lasker 1970; Shchepkin 1971a, b; Schevchenko 1972; Shul'man 1974; Tyler and Dunn 1976; Wootton and Evans 1976; Lasker and Smith 1977; Diana and MacKay 1979; Delahunty and de Vlaming 1980; Patzner 1980; Hunter and Leong 1981). The seasonal accumulation of sufficient reserves may be a prerequisite for sexual maturity in some fishes (Iles 1974), and the amount of material stored may influence fecundity (Tyler and Dunn 1976). Reserves may also be used in migration (Robertson and Wexler 1960; Dotson 1978; Glebe and Leggett 1981 a, b), and, when used in spawning migrations, may contribute indirectly to reproduction.

Slobodkin (1962) and Calow (1977), however, noted that fat deposition may actually detract from reproduction, particularly when fat deposition and reproduction are concurrent. In such cases, reserves are often used instead for maintenance during periods of food scarcity (Calow and Jennings 1977), enhancing the opportunity to reproduce in the future. Some fishes seem to use reserves both for reproduction and maintenance, when spawning occurs during periods of food scarcity or fasting (Wilkins 1967; MacKinnon 1972; Iles 1974; Newsome and Leduc 1975; Foltz and Norden 1977; Dawson and Grimm 1980; Pierce et al. 1980; Glebe and Leggett 1981 a, b). The interpretation of such cases is complex, since reproduction and maintenance may be competing concurrently for reserves.

Roberts (1979) noted that fat was deposited seasonally around the viscera of two species of shallow-water rockfish, *Sebastes mystinus* and *S. melanops*. He suggested that the cycle of fat deposition and utilization was related to seasonal changes in the abundance of food and to reproduction.

In this paper we examine the seasonal relationship

[1]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA; present address: 3298 Madera Avenue, Oakland, CA 94619.

[2]Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132.

[3]Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

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between visceral fat volume and gonad volume in five offshore species of rockfish: *Sebastes entomelas*, *S. paucispinis*, *S. goodei*, *S. pinniger*, and *S. flavidus*. Based on Roberts' suggestion and the general literature on fat cycles in fishes, we expected to find complementary cycles of fat and gonad volume, indicating that reserves are used in reproduction. We used visceral fat volume as a convenient index of the timing and magnitude of seasonal changes in reserves, explicitly assuming that reserves stored elsewhere would change coincidentally (Delahunty and de Vlaming 1980). Since we did not measure total reserves, our data on visceral fat volume cannot be applied to quantitative studies of energy budgets, but are most useful for examining seasonal changes and making comparisons within a group of closely related species.

The use of gonadal volume as an index of reproductive activity requires some explanation. In males, gonadal volume is a good index of the timing of gametogenesis. In females of this live-bearing genus, however, gametogenesis is often reflected only in the initial increase of gonadal volume. Following fertilization (which may occur some time after copulation, due to sperm storage [Sorokin 1961; Echeverria 1981[4]; Boehlert and Yoklavich 1984]), ovarian volume continues to increase during a gestation period that lasts a month or so (Moser 1967). There may be some postzygotic nutrition of embryos during this time (Boehlert and Yoklavich 1984), but much of the increase in volume is due to the accumulation of water (Moser 1967). In some species of *Sebastes* that spawn more than once a year, gametogenesis takes place again late in the reproductive season of females. Among the species considered here, *S. paucispinis* and *S. goodei* are clearly multiple spawners (Moser 1967; MacGregor 1970), and Echeverria[5] has presented some evidence for multiple spawning in *S. pinniger*.

MATERIALS AND METHODS

Party boat and commercial rockfish catches were sampled weekly, as a part of a large-scale study, by personnel from the National Marine Fisheries Service (Tiburon Laboratory) and the California Department of Fish and Game, at northern California fishing ports between Crescent City (lat. 41°N) and Morro Bay (35°N). The species sampled depended on the day's catch. Samplers measured the total length of each specimen to the nearest millimeter and removed the viscera and gonads for preservation in 10% Formalin[6] in seawater.

In the laboratory, fat tissue was dissected from the viscera and its volume estimated by water displacement in graduated cylinders. In some samples, a small amount of fat had liquified. The volume of this liquid was estimated and added to total fat volume. Gonads were also removed and their volume measured as above. The state of development of ovaries and testes was scored according to indices based mainly on gonad morphology and coloration (Moser 1967; Gunderson et al. 1980). Histological preparations of small gonads were used to confirm sex and state of maturity. Data for species, sex, total length, stage of maturity, and fat and gonad volume were stored using a computer.

Data on visceral fat volume were analyzed for collections made between March 1980 and February 1981, inclusive. Measurements of gonad volume were begun in June 1980 and continued until May 1981 to obtain a full year of data. For each species, data were pooled over all ports of collection and divided quarterly, as follows: spring (March-May), summer (June-August), fall (September-November), and winter (December-February). Quarterly division of data gave good sample sizes for most seasons, yet still allowed seasonal separation. Primary production is relatively low off California during fall and winter, but is greater during most of spring and summer, when coastal upwelling occurs (Bolin and Abbott 1963).

To facilitate comparisons, visceral fat volume and gonad volume were expressed as log-transformed power-function regressions of volume on fish length. The power equation is:

$$V = aL^b,$$

where V is volume, L is total length, and a and b are estimated parameters. This equation is often used to express the relationship between volumetric measures, such as fecundity, and linear measures, such as length (Bagenal 1978; Glebe and Leggett 1981a; de Vlaming et al. 1982). Logarithmic transformation to

$$\ln V = \ln a + b \ln L$$

[4]Echeverria, T. 1981. Maturity in six species of rockfish (Pisces, Scorpaenidae, *Sebastes*). [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

[5]Echeverria, T. 1983. Maturity and seasonality of the rockfishes (Scorpaenidae: *Sebastes*) of central California. Unpubl. manuscr., 60 p. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

allows the use of standard least-squares regression techniques, and stabilizes variances (Bagenal 1978). Thus, rather than using ratios of fat or gonad volume to fish weight or length, which can be biased by allometric relationships between the measurements (Bagenal 1978; de Vlaming et al. 1982), we employed empirically derived regression lines. The use of power equations also allowed us to test hypotheses with standard statistical procedures. Regressions were calculated for each sex during each season. Although most of the analyses were for adults, seasonal regressions of visceral fat volume were also computed for juveniles when samples were large.

Differences between regressions of fat or gonad volume were tested by analysis of covariance, using the ratio:

$$F = \frac{(N - 4)\,(SS_{com.} - SS_1 - SS_2)}{2\,(SS_1 + SS_2)}$$

where SS_1 and SS_2 are the residual sums of squares about the separate regressions, $SS_{com.}$ is the residual sum of squares for a common regression, and N is the number of specimens (Kleinbaum and Kupper 1978). When regressions differed significantly, the direction of differences was assessed by examining the positions of the regression lines and of calculated volumes at mean fish length. We chose to display only the calculated volumes at mean length, to simplify the presentation of data. The mean of ln (total length) was determined for all specimens of a sex and species included in the annual analysis. For each season and sex, the estimated value of ln (volume) at the mean of ln (length) (designated $\hat{Y}$) was calculated from the appropriate regression. We intend these point values to be used only for making comparisons within our data. The regression lines themselves best represent fat or gonad volume, and we present the parameters for these regressions. See Guillemot (1982) for scatter diagrams of raw data and regression plots.

The estimated values of fat volume at mean length were also used in an index of the relative amplitude of fat cycles. This index was the antilog of the difference between estimated ln (fat volume) in peak and low seasons, and is equivalent to the ratio of peak season:low season fat volume.

We compared fat cycles of males and females within a species by qualitatively noting differences in the timing and amplitude of fat cycles, and by statistically comparing fat regressions during peak and low seasons of fat volume. The latter comparisons were carried out by analysis of covariance, as above.

In comparing fat cycles among species, we noted differences in the timing of fat cycles and differences in the amplitude of cycles. We also assessed differences in the absolute volume of fat stored by applying analyses of covariance to the peak-season fat regressions of the different species.

RESULTS

Seasonal Cycles of Fat and Gonad Volume in Adults

In most seasons, moderate to low correlations (0.5 and below) existed between ln (visceral fat volume) and ln (total length), indicating a fair amount of scatter about the regressions (Table 1). Lower correlations occurred mainly in seasons of low fat volume (cf. Fig. 1). The slopes of most regressions were not significantly different from 3.0 (Table 1), indicating a proportionate relationship between fat volume and fish length. Slopes significantly smaller than 3 occurred in seasons of low fat volume (winter and spring), and in general slopes from seasons of low fat volume were smaller than those from seasons of higher fat volume. During seasons of low fat volume, fish of all sizes tended to have little fat, accounting in part for some of the lower correlations. Some slopes were significantly greater than 3 during seasons of high fat content (*S. entomelas* females, *S. paucispinis* males, *S. pinniger* females, and *S. flavidus* females), indicating disproportionately greater fat content in larger fish. Correlations between ln (gonad volume) and ln (total length) were generally high (Table 2), and showed no marked relation with season (Fig. 2). Below, we first examine the fat and gonad cycles for adults of each species separately, and then briefly compare the cycles of different species.

Sebastes entomelas

Visceral fat content changed significantly during the year in both male and female *S. entomelas* (Fig. 1). In females, where all seasonal regressions of ln (visceral fat volume) on ln (total length) differed significantly from each other, fat content increased from a low in spring to a peak in fall, and then declined in winter (Fig. 1). In males, neither the spring and winter nor the summer and fall fat regressions differed significantly (Fig. 1). Visceral fat volume in males increased after spring to a peak spread through summer and fall, and then declined in winter (Fig. 1). During the fall, when both sexes had large volumes of visceral fat, fat content of males barely

TABLE 1.—Seasonal regressions of ln (visceral fat volume, ml) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California. Slopes significantly different from 3 are indicated (? = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$).

Species and season	Females				Males			
	Sample size	Intercept	Slope	r	Sample size	Intercept	Slope	r
S. entomelas								
Spring	118	'21.752	3.845	0.240	88	−12.267	2.341	0.138
Summer	102	−23.875	4.335*	0.578	58	−32.427	5.795?	0.456
Fall	81	−28.715	5.184**	0.581	57	−20.654	3.908	0.459
Winter	163	−18.442	3.400	0.428	84	−19.524	3.538	0.251
S. paucispinis								
Spring	117	−10.334	1.988?	0.314	115	−17.544	3.150	0.443
Summer	116	−16.415	2.982	0.576	127	−16.120	2.978	0.553
Fall	75	−12.957	2.500	0.462	101	−24.053	4.259**	0.693
Winter	82	−1.269	0.633***	0.165	83	−9.847	1.942*	0.389
S. goodei								
Spring	193	−12.741	2.220	0.272	51	−14.555	2.671	0.281
Summer	219	−10.780	2.027	0.221	80	−11.827	2.299	0.403
Fall	140	−14.895	2.763	0.499	68	−17.686	3.228	0.334
Winter	183	0.253	0.155***	0.020	55	0.783	−0.026?	−0.002
S. pinniger								
Spring	23	−16.134	2.980	0.400	38	−16.581	3.006	0.445
Summer	61	−28.391	4.957***	0.786	103	−17.213	3.152	0.455
Fall	32	−24.771	4.453	0.579	37	−14.859	2.825	0.593
Winter	18	−24.371	4.289	0.529	14	−28.849	5.063	0.538
S. flavidus								
Spring	73	8.221	−1.038**	−0.099	71	−18.255	3.298	0.259
Summer	143	−24.044	4.323**	0.605	88	−10.960	2.152	0.240
Fall	147	−14.050	2.771	0.468	112	−8.652	1.777	0.212
Winter	69	−2.946	0.743*	0.092	72	−14.442	2.575	0.227

exceeded that of females. Fat regressions at the low point in spring did not differ significantly (Table 3).

As expected, gonad volume changed significantly during the year in both sexes of *S. entomelas* (Fig. 2). In males, the volume of testes increased dramatically from a low in spring to a peak in summer, and then declined through fall and winter (Fig. 2). In females, the volume of ovaries increased very slightly between spring and summer, and then increased greatly in fall and winter (Fig. 2).

Sebastes paucispinis

Visceral fat volume changed significantly during the year in males and females of *S. paucispinis* (Fig. 1). In females, fat content did not change significantly between spring and summer, but increased from summer to a peak in fall, to decline slightly in winter (Fig. 1). In males, visceral fat accumulated between spring and summer, remained about constant from summer to fall, and declined in winter (Fig. 1). During the nominal peak season in fall, fat content of females was significantly greater than that of males, while the regressions for fat content during the nominal low points in spring did not differ significantly (Table 3).

Ovarian volume in *S. paucispinis* reached its low point during summer, increased with vitellogenesis in fall, increased again with embryogenesis and/or further vitellogenesis in winter, and then declined in spring (Fig. 2). The volume of testes increased from spring into summer, continued to increase slightly in fall, and declined in winter (Fig. 2).

Sebastes goodei

Visceral fat volume in female *S. goodei* increased from spring through summer to a peak in fall, and declined in winter (Fig. 1). In male *S. goodei*, visceral fat volume increased from low levels in spring to a peak in summer, declined slightly in fall, and decreased again in winter (Fig. 1). The fat content of females during their fall peak exceeded that of males during their summer peak, while there was no significant difference in fat content during the low seasons of spring for females and winter for males (Table 3).

Ovarian volume increased slightly between spring and summer in females of *S. goodei*, and then grew more rapidly through fall and winter (Fig. 2). The volume of testes increased greatly between spring and summer in males of *S. goodei*, and then declined through fall and winter (Fig. 2).

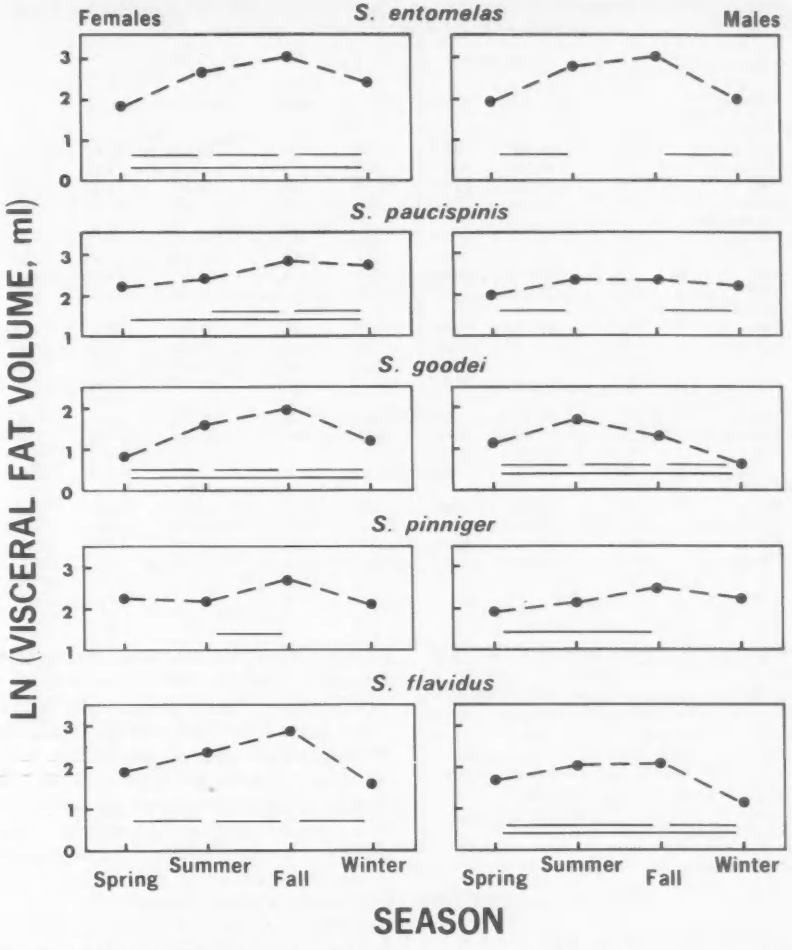

FIGURE 1. – Seasonal variation of visceral fat volume in adults of five species of *Sebastes* from northern and central California. For each species and sex, points are estimates of ln (fat volume) at the overall average of ln (total length) for specimens of that species and sex examined during the year. Estimates were derived from the seasonal regressions of ln (visceral fat volume) on ln (total length) (Table 1). A horizontal line between two seasons means that the fat regressions for those two seasons differed significantly ($P \leq 0.05$) by analysis of covariance. The upper of the two rows of horizontal lines are for adjacent seasons in the graph. The lower horizontal line is for winter and spring. The absence of a horizontal line means that the regressions did not differ significantly. Annual averages of ln (total length, mm) are *S. entomelas* females, 6.13, and males, 6.08; *S. paucispinis* females, 6.31, and males, 6.20; *S. goodei* females, 6.11, and males, 5.88; *S. pinniger* females, 6.11, and males, 6.14; and *S. flavidus* females, 6.11, and males, 6.04. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

TABLE 2.—Seasonal regressions of ln (gonad volume, mL) on ln (total length, mm) in adults of five species of *Sebastes* from northern and central California.

Species and season	Females				Males			
	Sample size	Intercept	Slope	r	Sample size	Intercept	Slope	r
S. entomelas								
Spring	217	−36.259	6.226	0.787	93	−40.725	6.738	0.709
Summer	17	−50.148	8.148	0.908	18	−42.341	7.386	0.644
Fall	85	−58.734	10.187	0.781	33	−10.442	1.930	0.191
Winter	177	−40.049	7.249	0.532	115	−18.856	3.207	0.403
S. paucispinis								
Spring	113	−26.341	4.541	0.640	163	−36.055	5.933	0.855
Summer	78	−34.265	5.767	0.919	105	−36.360	6.130	0.807
Fall	78	−37.533	6.386	0.833	118	−28.802	4.935	0.845
Winter	118	−34.058	5.946	0.647	127	−17.757	3.014	0.508
S. goodei								
Spring	146	−34.372	5.961	0.785	60	−20.612	3.552	0.332
Summer	166	−32.127	5.617	0.798	63	−12.733	2.386	0.283
Fall	176	−17.064	3.293	0.460	93	−29.433	5.095	0.772
Winter	184	−27.812	5.151	0.495	71	−17.172	2.886	0.214
S. pinniger								
Spring	21	−23.843	4.181	0.694	35	−49.963	8.230	0.799
Summer	22	−51.129	8.611	0.902	43	−60.352	10.175	0.939
Fall	31	−50.164	8.448	0.889	40	−45.336	7.564	0.845
Winter	21	−34.798	6.022	0.538	14	−65.227	10.657	0.904
S. flavidus								
Spring	100	−29.422	5.083	0.707	138	−31.837	5.228	0.499
Summer	83	−33.961	5.892	0.852	50	−54.152	9.204	0.759
Fall	162	−47.425	8.155	0.822	134	−38.906	6.649	0.690
Winter	53	−30.680	5.592	0.575	80	−23.743	3.927	0.555

TABLE 3.—Comparisons of fat volume between males and females during peak and low fat seasons in five species of *Sebastes*. If not defined statistically, peak and low seasons were selected on the basis of regression positions. $\hat{Y}$, the estimated ln (fat volume) at the overall average of ln (total length), is presented as an indication of regression position (Fig. 1). If male and female fat regressions differed significantly ($P \leq 0.05$) by analysis of covariance, their relative fat volumes are indicated. NS denotes regressions that did not differ significantly.

Species	Females		Males		Comparison
	Season	$\hat{Y}$	Season	$\hat{Y}$	
S. entomelas					
Peak	Fall	3.07	Fall	3.09	♂ > ♀
Low	Spring	1.82	Spring	1.96	NS
S. paucispinis					
Peak	Fall	2.81	Fall	2.35	♀ > ♂
Low	Spring	2.20	Spring	1.99	NS
S. goodei					
Peak	Fall	1.98	Summer	1.70	♀ > ♂
Low	Spring	0.82	Winter	0.63	NS
S. pinniger					
Peak	Fall	2.69	Fall	2.49	NS
S. flavidus					
Peak	Fall	2.87	Fall	2.08	♀ > ♂
Low	Winter	1.59	Winter	1.12	NS

Sebastes pinniger

Cycles of visceral fat volume were poorly defined in *S. pinniger*. In females, only the summer and fall fat regressions differed significantly, suggesting a peak in fat content during the fall (Fig. 1). In males, no two consecutive seasons differed significantly in fat content, and the only two seasons that differed significantly at all were spring and fall (Fig. 1). Thus, males may also have had peak fat content during fall, but their fat cycle was not pronounced. The visceral fat content of males and females did not differ significantly during their apparent fall peaks (Table 3).

The ovarian cycle of *S. pinniger* was also poorly defined in our data. Ovaries increased significantly in volume between spring and summer (Fig. 2). No other seasons differed significantly, but a peak in winter is indicated in Figure 2. In males, gonadal volume increased dramatically from spring to a peak in summer, remained fairly high in fall, and declined in winter (Fig. 2).

Sebastes flavidus

Visceral fat volume in female *S. flavidus* increased from spring through fall, and then declined in winter (Fig. 1). Male *S. flavidus* exhibited a gradual increase in fat content between spring and fall, followed by a decline to minimal fat levels in winter (Fig. 1). Fat content of females exceeded that of males during their fall peaks, and the difference in fat content during their winter lows was not significant (Table 3).

Ovarian volume in *S. flavidus* showed a pattern similar to most of the rest of the species: an increase

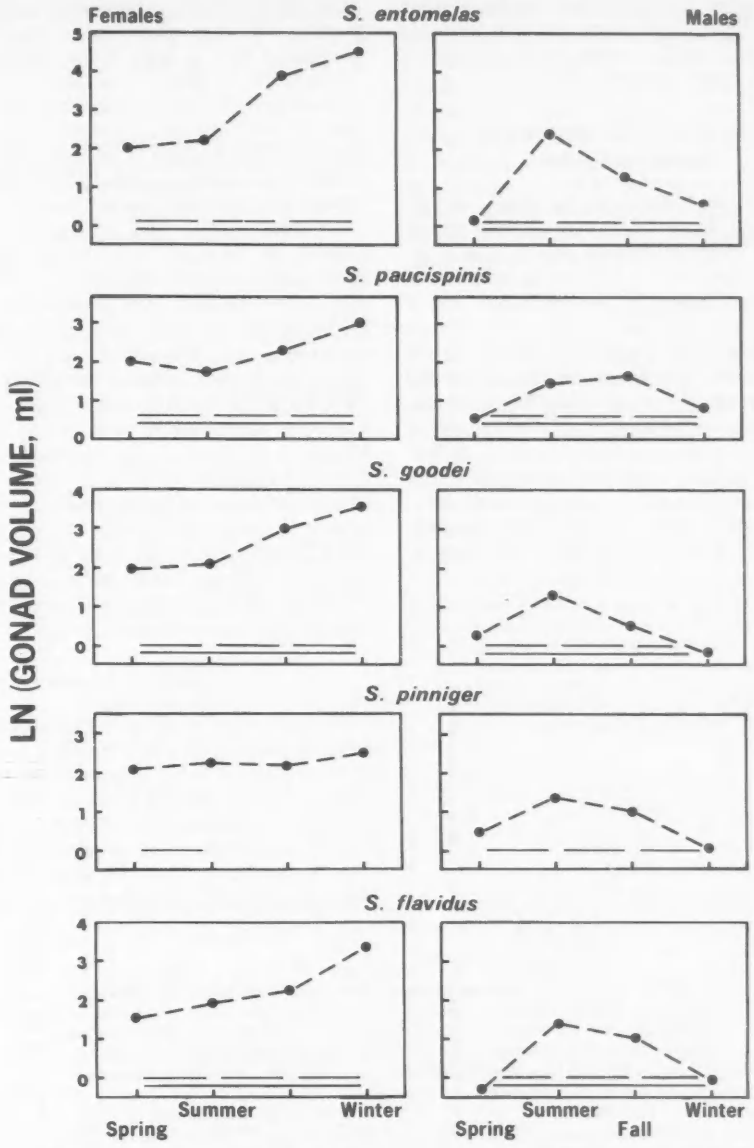

FIGURE 2. – Seasonal variation of gonad volume in adults of five species of *Sebastes* from northern and central California, as in Figure 1. Averages of ln (total length, mm) used in estimating gonadal volume are *S. entomelas* females, 6.14, and males, 6.06; *S. paucispinis* females, 6.24, and males, 6.17; *S. goodei* females, 6.09, and males, 5.88; *S. pinniger* females, 6.20, and males, 6.13; and *S. flavidus* females, 6.09, and males, 6.04. Seasons: spring (March-May 1981), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

from low volume in spring to peak volume in winter (Fig. 2). In males, the volume of testes increased from spring to a peak in summer, declined slightly in fall, and fell greatly in winter (Fig. 2).

Summary and Comparison of Adult Fat Cycles

In all species studied, visceral fat volume was high, if not at a peak, during fall. In males, fat content was usually high during summer as well. In male *S. entomelas*, *S. paucispinis*, and *S. flavidus*, summer and fall fat content did not differ significantly, and in male *S. goodei* the fat content in summer was actually greater than in fall. Summertime fat content was relatively high in female *S. entomelas*, *S. goodei*, and *S. flavidus*, but in females of all species the fat content increased to a peak in fall. Winter and spring were usually the seasons of low fat volume in both sexes. Little pattern existed in *S. pinniger*, except that fat volume appeared to reach a peak in fall.

Both the relative amplitude of fat cycles and peak fat volume differed among the species and sexes. In male and female *S. entomelas*, *S. goodei*, and *S. flavidus*, the fat volume of average-sized fish changed by about a factor of three during the year (Table 4). The amplitude of the fat cycle was lower in *S. paucispinis* and *S. pinniger*, where there was less than a twofold change in fat content between peak and low seasons (Table 4). Among females, *S. entomelas* and *S. flavidus* generally had higher peak fat volumes than the other species (Table 5). Among the other three species, peak fat content of females seemed to decrease from *S. pinniger* to *S. paucispinis* to *S. goodei* (Table 5). Females of *S. entomelas* and *S. flavidus*, then, possessed high-volume, high-amplitude fat cycles, while *S. pinniger* and *S. paucispinis* had low-volume, low-amplitude fat cycles, and *S. goodei* showed low volume and relatively high amplitude. The peak fat volume in male *S. entomelas* far exceeded that of the remaining species, most of which had relatively similar fat-length relationships during peak seasons (Table 5). Thus among males, only *S. entomelas* showed a high-volume, high-amplitude fat cycle. Males of *S. flavidus* and *S. goodei* possessed fat cycles of low volume and moderately high amplitude, and *S. paucispinis* and *S. pinniger* had cycles of low volume and low amplitude, like the females of these species.

TABLE 4.—Relative amplitude of fat cycles in five species of *Sebastes*. The ratio of estimated peak season: low season fat volume is presented for each species and sex, and is used as an index of cycle amplitude. Ratios are the antilogs of the differences between estimated ln (fat volume) at the average of ln (total length) in peak and low fat seasons (Fig. 1, Table 3).

	Amplitude	
Species	Females	Males
S. entomelas	3.50	3.10
S. paucispinis	1.83	1.44
S. goodei	3.20	2.91
S. pinniger	1.67	1.84
S. flavidus	3.61	2.64

Fat Cycles in Juveniles

Fat cycles were examined in juveniles of male and female *S. paucispinis*, and of female *S. pinniger* and *S. flavidus*, where seasonal sample sizes were large enough to permit analysis (Table 6). In *S. paucispinis*, juvenile females appeared to reach a peak in fat content during winter, but in juvenile males there were no significant differences among the seasonal regressions (Fig. 3). In *S. pinniger*, juvenile females

TABLE 5.—Comparisons of the peak-season regressions of ln (fat volume) on ln (total length) for different species of *Sebastes*. Comparisons were made by analysis of covariance. For significantly differing regressions ($P \leq 0.05$), the comparative fat volumes are indicated (based on the positions of the regressions, cf. Fig. 1, Table 1), unless intersecting lines made position difficult to interpret. NS denotes regressions that did not differ significantly.

	S. paucispinis	*S. goodei*	*S. pinniger*	*S. flavidus*
Females				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	NS	NS
S. paucispinis		*S.pa.* > *S.g.*	NS	*S.pa.* < *S.f.*
S. goodei			*S.g.* < *S.pi.*	*S.g.* < *S.f.*
S. pinniger				*S.pi.* < *S.f.*
Males				
S. entomelas	*S.e.* > *S.pa.*	*S.e.* > *S.g.*	*S.e.* > *S.pi.*	*S.e.* > *S.f.*
S. paucispinis		intersection	*S.pa.* < *S.pi.*	intersection
S. goodei			NS	NS
S. pinniger				NS

possessed little fat in the spring, and higher levels in summer through winter (Fig. 3). Fat content in juveniles of female *S. flavidus* peaked in fall (Fig. 3).

TABLE 6.—Seasonal regressions of ln (visceral fat volume, mL) on ln (total length, mm) in juveniles of three species of *Sebastes* from northern and central California.

Species and sex	Season	Sample size	Intercept	Slope	r
S. paucispinis					
females	Spring	140	−19.637	3.510	0.325
	Summer	138	−26.793	4.669	0.455
	Fall	55	−23.626	4.189	0.419
	Winter	67	−29.508	5.205	0.719
males	Spring	92	−10.309	1.976	0.157
	Summer	86	−22.626	3.969	0.362
	Fall	10	−48.866	8.324	0.599
	Winter	21	−27.486	4.818	0.766
S. pinniger					
females	Spring	41	−21.012	3.655	0.402
	Summer	76	−21.794	3.859	0.624
	Fall	37	−36.539	6.383	0.875
	Winter	20	−18.568	3.345	0.651
S. flavidus					
females	Spring	21	−22.796	4.080	0.388
	Summer	70	−8.502	1.642	0.260
	Fall	53	−36.450	6.558	0.639
	Winter	19	−9.906	1.848	0.361

Thus, in three of the four groups analyzed, fat content of juveniles varied during the year. The timing of the apparent cycles was similar to that of adults. The amplitude of the fat cycle in juveniles of female *S. paucispinis* and *S. pinniger* (less than twofold change in fat volume) was similar to adult amplitude. In female *S. flavidus*, the amplitude of the fat cycle in juveniles (less than twofold change) was lower than in adults. As adults, *S. flavidus* showed high-amplitude fat cycles, while *S. paucispinis* and *S. pinniger* showed low-amplitude cycles.

DISCUSSION

Clear cycles of visceral fat volume and gonadal volume occurred in both sexes of *S. entomelas*, *S. paucispinis*, *S. goodei*, and *S. flavidus*. The fat cycles of male and female *S. pinniger* were less well-defined, as was the gonadal cycle of female *S. pinniger*. Many of the female *S. pinniger* we examined were relatively small adults. This may account, at least in part, for the small and ill-defined fat and gonad cycles, as the fat cycles of female *S. flavidus* increased in amplitude from juveniles to adults.

Visceral fat volume generally increased propor-

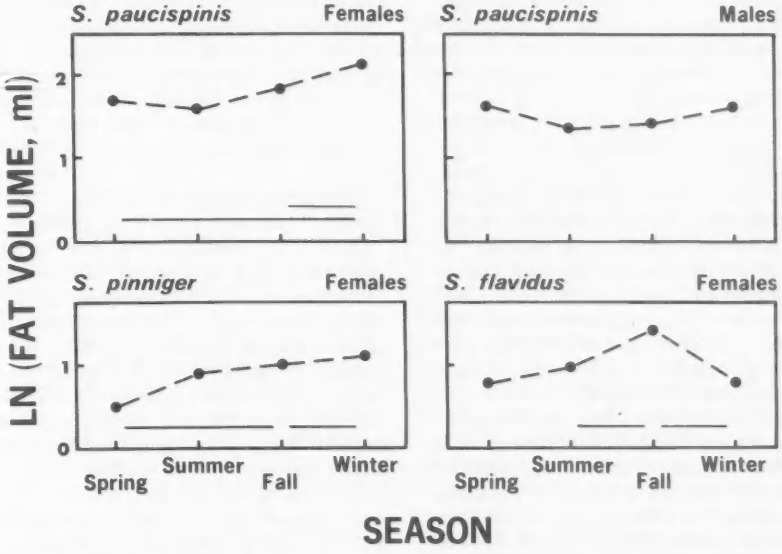

FIGURE 3.—Seasonal variation of visceral fat volume in the juveniles of five species of *Sebastes*, ≡ in Figure 1. Averages of ln (total length, mm) used in estimating fat volume are *S. paucispinis* females, 6.08, and males, 6.04; *S. pinniger* females, 5.88; and *S. flavidus* females, 5.78. Seasons: spring (March-May 1980), summer (June-August 1980), fall (September-November 1980), and winter (December 1980-February 1981).

tionately with fish volume, since most slopes of ln (fat volume) on ln (length) were near 3. Slopes smaller than 3 occurred in those seasons when fish of all sizes had little fat. Some slopes during seasons of high fat volume were significantly greater than 3, indicating that larger fish had disproportionately greater fat volume than smaller fish. This was particularly true of, but not limited to, the species and sexes with high-magnitude fat cycles (males and females of *S. entomelas* and females of *S. flavidus*). It would be interesting to discover whether larger females of *S. pinniger* have high-amplitude fat cycles, since the slopes of the fat regressions for female *S. pinniger* were relatively high.

The dependence of fat volume on fish size and season of collection, while applicable on average, does not apply to every individual. The scatter about the regressions of fat volume on length was large. Some of the scatter was probably due to errors in measurement, but a large part was real. We have observed large differences in the amount of visceral fat among fish of the same size and sex in the same collection. The reasons for such variation may be difficult to resolve, since it is difficult to know the history of individuals collected in the field.

However, our data were adequate in most species to detect seasonal changes on average. We wanted to compare the timing of fat cycles and gonad cycles, and thus learn something of the function of fat storage in rockfish. Our initial hypothesis was that stored fat would be used in reproduction, based on Roberts' (1979) observations.

The data for males do not support this hypothesis. Fat and gonad cycles were nearly coincident, with peaks in both cycles occurring in fall and/or summer and lows in winter/spring. Thus the energy for gonadal growth was probably derived from current ingestion, not from material previously stored as fat. Maximum somatic growth also coincides with the summertime growth of testes and fat deposits (e.g., Love and Westphal 1981), so all three processes may be competing for energy consumed during this time.

The situation is more complicated in females. Some fat was deposited between spring and summer in females of *S. entomelas*, *S. goodei*, and *S. flavidus*, and females of all species gained fat between summer and fall. Some gonadal growth took place between spring and summer in females of all species except *S. paucispinis*. In all but *S. pinniger*, however, ovarian volume increased steadily between summer and winter. The growth of ovaries through fall was due largely to vitellogenesis, while the greater growth of ovaries into winter was due primarily to embryogenesis and hydration of ova (Moser 1967). Additional vitellogenesis probably occurred during winter in the multiple spawners, *S. paucispinis* and *S. goodei* (Moser 1967; MacGregor 1970).

In females, then, fat deposition usually began in summer, perhaps slightly before the initiation of vitellogenesis, but continued into the main period of vitellogenesis between summer and fall. Thus, like males, females of these species deposited fat more or less concurrently with gonadal maturation and somatic growth. The depletion of visceral fats occurred between fall and spring in females of most species, during and after gestation. It is possible that fat reserves are used for the maturation of additional ova in multiple spawners or are involved in the nutrition of embryos (Boehlert and Yoklavich 1984), but as in males, reserves are not used in the initial development of gonads.

There were two main differences in the fat cycles of males and females: females usually had larger fat cycles than males, and the peak fat volume of females occurred in fall, while fat volume in males usually reached a plateau that spread through summer and fall. It is possible that courtship activity in males (Helvey 1982) draws energy from fat deposition between summer and fall, or that this activity draws time from feeding. As a result, females may continue to fatten after fat deposition ceases in males. It is also possible that females require more reserves in winter and they somehow are able to acquire these extra reserves.

The synchronous depletion of reserves in males and females, however, indicates a common function for such reserves. We suggest two possible functions:

First, some rockfish may migrate during the period of fat depletion. Love (1981) presented evidence for seasonal movements in *Sebastes paucispinis* and *S. entomelas* off southern California, but had no data on the extent or direction of movement. Females of *S. alutus* undertake seasonal migrations covering as much as 300 m of depth (summarized in Gunderson 1977). Lenarz (pers. obs.) found evidence of seasonal movement in female *S. jordani*. Several species of rockfish undertake little or no seasonal migration, including *S. flavidus* from shallow waters off Alaska (Carlson and Barr 1977). Since seasonal migrations in rockfish may not be long and seem to occur primarily in females, we suggest that other possibilities be ruled out before accepting migration as a major use of fat reserves.

Second, we suggest that fat reserves are used for maintenance during wintertime periods of reduced food availability. Fattening, as well as growth and

initial gametogenesis, occurs during and shortly after the spring-summer upwelling period, and depletion occurs during and after a time of lower primary production (Bolin and Abbott 1963). Roberts (1979) noted that several species of inshore rockfish near Monterey consumed more food during the summer, when macroplankton (euphausiids) and juvenile rockfish were abundant. During the nonupwelling season, juvenile rockfish and macroplankton were less abundant, and adult rockfish consumed less food. Love and Westphal (1981) found less food in the stomachs of *S. serranoides* during the nonupwelling season near Morro Bay. Gunderson (1977) noted a "summer feeding season" in *S. alutus*. Hobson and Chess[7], however, found the gelatinous prey of *S. mystinus* to be more abundant during nonupwelling periods off northern California. There is only limited information on the seasonal food habits of the five species studied here. *Sebastes paucispinis* is largely piscivorous (Phillips 1964), while *S. entomelas*, *S. goodei*, *S. pinniger*, and *S. flavidus* feed on macroplankton and small fish (Phillips 1964; Pereyra et al. 1969; Brodeur 1982). Brodeur (1982) examined seasonal changes in the diets of *S. flavidus* and *S. pinniger*, and found that food consumption declined during winter in *S. pinniger*, but not in *S. flavidus*. However, Carlson and Barr (1977) found a pronounced decline in activity during winter in *S. flavidus* off Alaska, suggesting seasonal changes in feeding. This hypothesis can be examined with concurrent data on food consumption and fat volume. It is not mutually exclusive with other functions of fat reserves, since some fat could also be used for migration, nourishment of embryos, or maturation of additional ova in multiple spawners.

The wintertime use of reserves for maintenance, however, is consistent with the overall pattern of long life and repeated reproduction in rockfish (as discussed also by Gunderson [1977]). As suggested by Slobodkin (1962) and Calow (1977), summertime fat deposition may exact a cost in current reproduction (if more gametes could be packed into rockfish abdomens) or in future increases in gamete capacity (through additional growth), but may help to ensure survival.

An interesting result of our study was the difference in magnitude of fat cycles among species, which was particularly evident in females. These differences are correlated with both the frequency of spawning and geographical distributions of the species. Females of *S. entomelas* and *S. flavidus* had fat cycles of high amplitude and volume, probably spawn only once a year (Westrheim 1975; Echeverria footnote 5), and have northerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). On the other hand, *S. paucispinis* and *S. goodei* had fat cycles of low amplitude and/or volume, spawn more than once a season, at least in southern California, and have southerly distributions (Phillips 1957, 1964; Gunderson and Sample 1980; Adams 1980). The case with *S. pinniger* is unclear. Females seemed to have low-amplitude fat cycles, but the small sample and small sizes of females in the samples make conclusions tenuous. Echeverria (footnote 5) has some evidence for multiple spawning in *S. pinniger*. If so, its northerly distribution would be inconsistent with the pattern seen in the other species. We will restrict our discussion to the remaining four species, although further studies of *S. pinniger* may be instrumental in evaluating the suggestions we make below.

The small fat cycles of multiple spawners are probably not caused by their potentially greater reproductive output, since fat deposition stops long before the maturation of additional batches of ova. It seems more likely that the magnitude of the fat cycle, frequency of spawning, and geographical distribution are all related. Boehlert and Kappenman (1980) suggested that year-round spawning in southern populations of *S. diploproa* served to increase reproductive output in response to annual variation in the survival of planktonic larvae. Multiple spawning in southern populations and species may also be a response to the more even seasonal distribution of upwelling in southern vs. northern areas of the northeastern Pacific (Bakun et al. 1974; Parrish et al. 1981; Smith 1978), as it affects planktonic larvae. However, the more restricted upwelling season in northern waters may also lead to larger and better defined seasonal variation in the food supply of adults. A more pronounced summertime pulse of food may enable northerly species like *S. entomelas* and *S. flavidus* to store large amounts of fat. Similarly, a more pronounced decline in food during winter may make the accumulation of such reserves necessary, and preclude the maturation of additional batches of ova. On the other hand, a more even seasonal distribution of food in the south may enable southerly species like *S. paucispinis* and *S. goodei* to produce additional batches of ova during winter, and may also reduce the need for wintertime reserves. These suggestions are speculative, but it should be possible to compare the seasonal variation of food consumption in species with northern vs. southern distributions.

[7]Hobson, E. S., and J. R. Chess. 1981. Seasonal patterns in trophic relationships of the blue rockfish, *Sebastes mystinus*. [Abstr.] Proceedings of the 1981 Western Groundfish Conference.

In summary, we suggest that seasonal changes in the availability of food are rather important in the life histories of rockfish. The summer storage and winter use of fat reserves, in near synchrony with growth and decline of gonad volume, indicate a wintertime paucity of food that is compensated by the use of material that was stored at the expense of fecundity or growth. Further study of seasonal feeding, fat deposition, and reproductive cycles, categorized by size and sex, would be useful in evaluating this hypothesis. Further, geographical comparisons of these cycles may illuminate some causes of differences in the life histories of rockfishes.

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THE POSSIBLE INFLUENCE OF WARM CORE GULF STREAM RINGS UPON SHELF WATER LARVAL FISH DISTRIBUTION

G. R. FLIERL[1] AND J. S. WROBLEWSKI[2]

ABSTRACT

We propose a simple one-dimensional model for examining the impact of warm core rings upon the larval fish distribution and abundance over the continental shelf off the northeastern United States. The model includes (in a cross-shelf averaged sense) the loss of larvae due to biological causes of mortality, the advective transport of larvae due to the mean down-shelf currents, and the changes in larval density produced by the on-shelf or off-shelf flows occurring when a ring approaches the shelf-slope front. The results of this highly idealized model indicate that the decreases in larval abundance caused by cross-shelf flows may be as large as those caused by biological factors and, furthermore, the effects are strongly dependent upon the rate of motion of the ring. A stationary ring may cause a 20 to 50% drop in abundance, depending on the strength and size of the ring and on the longshore velocity in the shelf water. When the ring is slowly moving, the impact can be even greater: a patch of larvae being advected downshelf by the longshore current could, when catching up to the back side of an eddy, essentially be swept off the shelf, decimating the patch.

Model predictions are compared with historical MARMAP data of larval cod and haddock density in the Georges Bank area. There does appear to be a relationship between the frequency of ring interaction with Georges Bank and the subsequent year-class strength of cod and haddock stocks. Thus we suggest that further investigation of the impacts of rings is warranted, both from the observational and the theoretical viewpoints. These studies should include detailed measurements in entrainment features, further analysis of ring-Bank interactions factoring in the closeness of the ring, the strength of its currents and its translation rate, and more detailed modelling of entrainment events and larval fish ecology.

Warm core rings form in the Slope Water region between the North American continental shelf and the Gulf Stream. These rings are eddies 100 to 200 km in diameter which result when a Gulf Stream meander separates from the main current. The potential impact of warm core rings upon the continental shelf ecosystem has become more apparent with routine satellite infrared images of the sea surface. Charts of sea surface temperature prepared from these images, e.g., Figure 1, (Halliwell and Mooers 1979; Chamberlin 1981) frequently show rings entraining cold water from the continental shelf. This interpretation is supported by ship observations and current meter records of water transport onto and off the continental shelf induced by warm core rings (Morgan and Bishop 1977; Smith 1978; Smith and Petrie 1982). Physical and biological oceanographers have long been aware of occasional intrusions of anomalously warm water onto Georges Bank (for a review, see Bolz and Lough 1981), which are now likely to be attributable to warm core ring activity. In 1961 Colton and Temple hypothesized that large numbers of larval fish of shelf species can be drawn off Georges Bank into warmer Slope Water where they succumb to unfavorable environmental conditions (c.f. Laurence and Rogers 1976).

The purpose of this paper is to examine theoretically the possible influence of warm core rings on the abundance and distribution of larval fish in continental shelf waters off the northeastern United States, in particular the shelf region associated with cod and haddock spawning on Georges Bank. Our study makes estimates of the advective losses of larvae because of the entrainment of shelf water by an eddy and predicts changes in larval density (the observable quantity in ichthyoplankton surveys) because of the onshore and offshore flows induced by a ring. We also consider the possible biological causes of mortality (e.g., predation, physiological death). In other words we wish to estimate the relative importance of the physical and biological losses via a mathematical model. While our model does not describe either in great detail, we feel that it does indicate the importance of ring-induced entrainment and the dependence of this effect upon the speed of translation of the ring, the width over which it interacts with the shelf, and the strength of its currents at the shelf break. We compare our model predictions of the spatial and temporal distributions of larval fish

[1]Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139.
[2]Department of Oceanography, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada; present address: Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME 04575.

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with the historical MARMAP (Maritime Resources Monitoring, Assessment and Prediction) data of larval cod and haddock distributions in the Georges Bank area (Smith et al. 1979). We also present an apparent relationship between years of low warm core ring activity and strong year classes in the fishery.

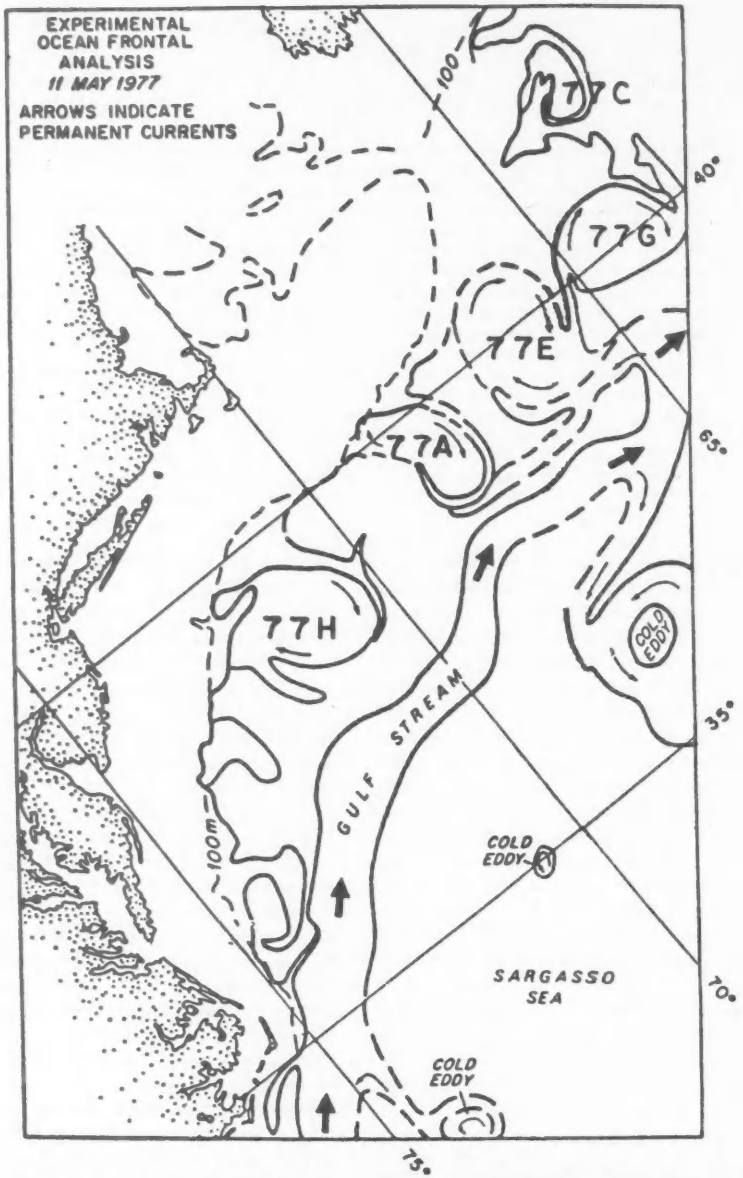

FIGURE 1.–Distribution of warm core rings off the U.S. northeast coast during the week of 11 May 1977. The chart was produced by the U.S. Naval Oceanographic Office from infrared satellite images.

Finally, we make recommendations for further investigations of the influence of warm core rings on the northeast coast marine ecosystem.

Our very simplified modelling approach to the problem of resolving biological distributions in a variable oceanic flow regime could, with proper reparameterizations, be applied to estimating the impact of rings on chemical distributions as well – an example would be determining the distribution of pollutants dumped in deepwater dumpsite 106. For variables which do not behave as passive particles in the flow, the model has limitations. Vertical migration behavior by fish larvae may play an important role in their distribution which is not resolved by our preliminary modelling. Other potentially important details, such as the mechanism for mixing on the shelf, have also not been included in this first, simplified calculation. Nevertheless, we feel that the results are extremely suggestive, indicating ways to examine existing data sets and hypotheses to be tested in future field studies.

THE MODEL

There are many possible approaches to modelling the effects of rings upon fish larvae, ranging from simple order-of-magnitude estimates to complex physical models which predict the mean and varying currents from winds, heating, topography, and coastlines. The water motions could then be coupled with complex biological models of spawning, predation, growth, and mortality. However, we are not yet at the stage where such a full-scale calculation is really justifiable; we do not understand enough about the physics of the shelf-slope region and the rings or enough about larval fish biology to ensure that only important processes are included and that these are being properly represented in our numerical model. In addition, the questions we wish to address are fairly simple ones: How large could the impact of rings upon larval fish populations be and how do these impacts depend upon the flow structure and translational speed of the rings? We, therefore, shall take the simplest approach to the problem of estimating our primary variable, the larval fish density (or abundance). The various processes which affect the population distribution will be represented in the model in an almost schematic form. The actual populations vary in all three dimensions and in time, but we shall include only the downstream and time variations in the model. Likewise, the actual current patterns are quite complicated and we choose only to represent the impact of the ring-induced currents by a specification of the flow at the outer edge of the shelf, with onshore flow ahead of the ring and offshore flow behind the eddy. The mean downshelf drift currents will also be included. The biological processes of predation, physiological mortality, and metamorphosis out of the planktonic larval stage will be represented simply as a loss rate μ which will be assumed to be independent of space or time. With these simplifications, the general equation governing the density $n(x,y,z,t)$ of the planktonic larvae can be reduced to a manageable form

$$\frac{\partial}{\partial t} n + \frac{\partial}{\partial x} un + \frac{\partial}{\partial y} vn + \frac{\partial}{\partial z} wn = -\mu n. \qquad (1)$$

We shall use the geometry shown in Figure 2 with x the downshelf coordinate, y the offshore coordinate,

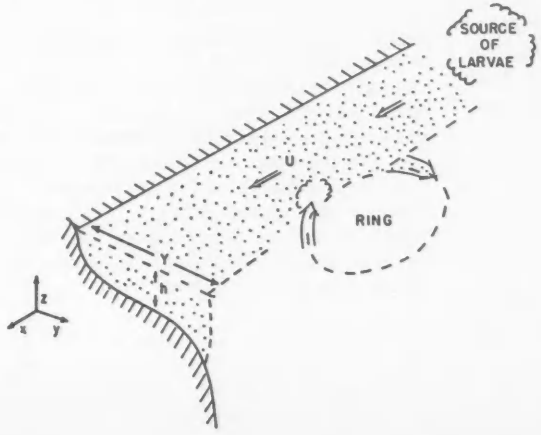

FIGURE 2. – Schematic diagram of the geometry assumed in the mathematical model. Y is the shelf width, h is the average depth, and U is the average longshore velocity of the shelf water.

and z positive upwards. We shall assume that there is a source of larvae somewhere upstream of $x = 0$, e.g., the spawning grounds on Georges Bank, leading to a specified flux of organisms into the domain at the $x = 0$ boundary. Alternatively, and more conveniently, the upstream spawning can be thought of as leading to a specified abundance of organisms $N_0(t)$ at $x = 0$.

Although we could, in principle, specify the three-dimensional currents and the source function N_0 from either measurements or models, the available data and models are not really adequate for this to be possible. We have chosen, therefore, to simplify the model further by averaging the larval fish density vertically and across the shelf

$$N(x,t) = \frac{1}{hY}\int_0^Y \int_{-h}^0 n(x,y,z,t)\,dz\,dy. \tag{2}$$

Here Y is the width of the shelf and h is the depth (both assumed independent of x). We can find the equation governing this N by averaging Equation (1) over the shelf width and depth, applying boundary conditions of zero flux through the upper and lower surfaces and the continent side of the domain. This gives

$$\frac{\partial}{\partial t}N + \frac{\partial}{\partial x}\left[\frac{1}{hY}\int_0^Y\int_{-h}^0 un\,dz\,dy\right] + \frac{1}{hY}\int_{-h}^0 v(x,Y,z,t)\,n(x,Y,z,t)\,dz = -\mu N. \tag{3}$$

The downstream variation of Y and h has been neglected although it is not too difficult to include it. The term representing downstream advection of larvae will be simplified by assuming that the cross-shelf mixing of larvae is sufficiently intense that n is uniform in y. The along-shelf advection term then becomes

$$\frac{\partial}{\partial x}\frac{1}{hY}\int_0^Y\int_{-h}^0 un\,dz\,dy \cong \frac{\partial}{\partial x}UN;$$

$$U(x,t) = \frac{1}{hY}\int_0^Y\int_{-h}^0 u(x,y,z,t)\,dz\,dy. \tag{4}$$

Similarly, we shall ignore vertical variations in n at the shelf edge so that the flux off the shelf becomes

$$\frac{1}{hY}\int_{-h}^0 v(x,Y,z,t)\,n(x,Y,z,t)\,dz \cong \frac{N_e V_0}{Y};$$

$$V_0(x,t) = \frac{1}{h}\int_{-h}^0 v(x,Y,z,t)\,dz. \tag{5}$$

Here $V_0(x,t)$ is the depth-averaged onshore-offshore flow (positive offshore) and N_e is the depth-averaged larval fish density in the water which is moving onto or off of the shelf. (Vertical migratory behavior which is somehow correlated with vertical shears would alter this parameterization of the outflowing flux of larvae.)

When there is onshore or offshore flow, the averaged velocity along the shelf cannot be constant. The variations in U can be calculated from the conservation of fluid volume integrated across the shelf

$$\frac{\partial}{\partial x}\left[\frac{1}{hY}\int_0^Y\int_{-h}^0 u\,dz\,dy\right] + \frac{V_0}{Y} = 0$$

$$\text{which implies } \frac{\partial U}{\partial x} = -\frac{V_0}{Y}. \tag{6}$$

Finally we must introduce a parameterization for the density of larvae carried on or off the shelf at the edge N_e in terms of the average density $N(x,t)$. It is assumed that the Slope Water pushed onto the shelf by the ring is devoid of shelf fish larvae. If we presume that this Slope Water mixes completely with the shelf water, then the water leaving the shelf carries larvae with density N, as sketched in Figure 2. These considerations suggest that the entrainment term can be modelled by

$$N_e = \begin{cases} 0 & \text{for } V_0 < 0 \\ N & \text{for } V_0 > 0 \end{cases}. \tag{7}$$

(Again, we must remark upon the limitations of the present calculation; certainly the shelf water is not thoroughly mixed and the density of the outflowing larvae is much more complicated and perhaps smaller on the whole than this formula would suggest. We hope that our results will spur further modelling and observational efforts to assess the processes we have been forced to represent so crudely.) When all of these simplifications are gathered together, the approximate equations for the average density of larvae $N(x,t)$ become

$$\frac{\partial}{\partial t}N + \frac{\partial}{\partial x}(UN) + \begin{cases} 0 & \text{for } V_0 < 0 \\ \dfrac{V_0 N}{Y} & \text{for } V_0 > 0 \end{cases} = -\mu N$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \tag{8}$$

with the boundary condition

$$N(0,t) = N_0(t). \tag{9}$$

STATIONARY EDDIES

In nature, there are pulses of larvae entering the domain as the fish spawn. In addition, the shelf-edge velocities $V_0(x,t)$ are changing as mesoscale eddies and Gulf Stream warm core rings impinge upon the shelf. We shall present in the section on moving eddies several numerical solutions of Equations (8) and (9), simulating this complex situation. However, in order to fully understand the importance of the rings and eddies in determining the fish larvae's spatial distribution, it is first useful to consider some simpler, analytically tractable cases. We shall begin by discussing the distributions which occur when the shelf-edge flows are not changing with time, i.e., the eddies are stationary. This problem also has bearing on the real situation south of Long Island, where rings may often stop for considerable lengths of time.

As a first example, consider the larval fish distribution which would occur in the absence of any biological loss processes ($\mu = 0$) and when the source term N_0 is independent of time. The resulting equations

$$\frac{\partial}{\partial x}(UN) = \begin{cases} -V_0 \dfrac{N}{Y} & \text{for } V_0 > 0 \\ 0 & \text{for } V_0 < 0 \end{cases},$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y} \tag{10}$$

can be solved readily

$$N = \begin{cases} N_0 \dfrac{U_0}{U} = \dfrac{N_0 U_0}{U_0 - \displaystyle\int_0^x \frac{V_0}{Y}} & \text{if } V_0 < 0 \quad (11a) \\ N_0 & \text{if } V_0 > 0 \text{ and } U_0 > \displaystyle\int_0^x \frac{V_0}{Y} \quad (11b) \\ 0 & \text{if } V_0 > 0 \text{ and } U_0 < \displaystyle\int_0^x \frac{V_0}{Y} \quad (11c) \end{cases}$$

where U_0 is the longshore velocity and N_0 is the (time-independent) population density at the upstream boundary $x = 0$. We can now see explicitly the effects of the physics alone upon the larval fish distribution. In the regions where the flow is onto the shelf (Equation (11a)), the shelf break boundary contribution to Equation (10) is zero. But the effects of the flow field are still felt in that the along-shelf flow is divergent. U increases downstream as water comes onto the shelf, spreading out the larvae and reducing their average density. In contrast, when the flow is offshore (Equations (11b) or (11c)), there are direct loss terms due to larvae being carried off the shelf. Some of the water flowing into a section are diverted offshore while some continues down the shelf, with the larvae separating in the same proportions. Thus, although there is a decreased flux down the shelf, this does not affect the density since there are no biological losses which need to be balanced by this flux. The net effect is that the physics by itself does not change the population density in regions of offshore flow (Equation (11b)). The only exception would occur when the offshore transport ($\int V_0\, dx$) is sufficiently strong so that all of the normal alongshore flow ($U_0\, Y$) is diverted off the shelf. In this case (Equation (11c)), the flow in regions farther down the shelf is reversed and the water moves up the shelf. Since this water is from regions without sources of larvae, the population density is zero.

By putting together these two results, we can construct a picture of the density of larvae in continental shelf water flowing past a stationary ring centered at $x = D$. This is shown in Figure 3. For these calculations we have used

$$V_0 = -A \frac{x - D}{L} \exp\left[\frac{1}{2} - \frac{1}{2}\frac{(x-D)^2}{L^2}\right] \tag{12}$$

with $A = 20$ cm/s the peak offshore velocity) and $L = 20$ km (so that roughly 80 km along the shelf is strongly influenced by the ring currents). This figure

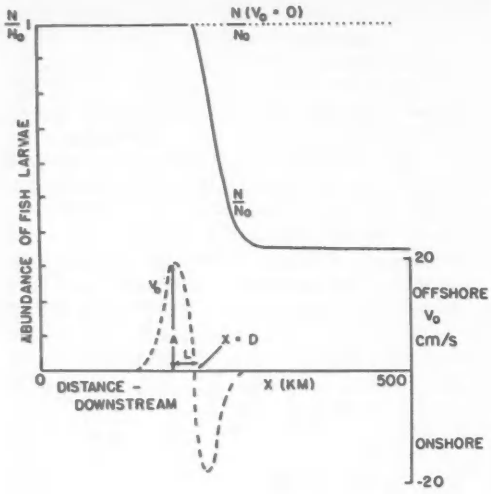

FIGURE 3.—The steady state abundance of fish larvae with distance along the shelf. This abundance is expressed as a fraction of the number of larvae continuously being produced at the spawning site, N_0. There is a 80 km wide, stationary eddy at the shelf edge, inducing onshore and offshore flows of 20 cm/s. The longshore velocity U_0 of the shelf water is 5 cm/s. Biological losses (μ) are set equal to zero. The dotted line shows the steady abundance of fish larvae with distance down the shelf when there is no eddy present.

shows only the spatial distribution of larval density in the water moving down the shelf, as affected by flow convergences or divergences associated with the physics of the ring. The flux of larvae off the shelf (not shown) is given by $V_0\, hN_0$ in the regions where V_0 is greater than zero and amounts in total to

$$\int_0^D V_0\, h\, N_0\, dx \cong A\, h\, L\, N_0\, e^{1/2}.$$

66% of the flux into the domain ($U_0\, N_0\, hY$) at $x = 0$. Next, we shall see that the physics and biology actually interact to produce a greater net impact than when either is considered separately.

For this second model problem, we shall still use a steady onshore and offshore flow pattern, but now include the biological loss term and the time-dependence in the source function N_0. When the flow is offshore or zero, the population distribution is given by

$$N(x,t) = N_0(t - \tau)\, e^{-\mu\tau} \tag{13a}$$

where the variable τ measures the length of time necessary to reach the point x from the upstream edge of the domain. In general τ is given by

$$\tau = \int_0^x \frac{dx'}{U(x')} \tag{13b}$$

where $U(x)$ can be found by integrating the mass conservation equation

$$U(x) = U_0 - \int_0^x dx' \frac{V_0(x')}{Y}. \tag{13c}$$

In the absence of ring-induced onshore-offshore flows ($V_0 = 0$), however, τ is just equal to x/U_0 and

$$N(x,t) = N_0 \left(t - \frac{x}{U_0}\right) e^{-\mu\, x/U_0}. \tag{13d}$$

The population at any downstream point lags that at the origin by the travel time x/U_0 and has also decayed exponentially during its travel. This solution is an important base case for understanding the distributions in a spawned patch which has not been impacted by rings.

When water is being drawn off the shelf, the along-shelf decay in concentration is again purely due to travel time, since the effect of losses off the shelf on the density is compensated for by the convergence. However the spatial density of the larvae is still noticeably altered by the offshore flow because the travel time necessary to reach any point is increased. This occurs because U is decreasing with x as a result of the advection of water off the shelf (as shown in Equation (13c)). Since U is less than U_0, the travel time τ in Equation (13b) is necessarily greater than that in the absence of the ring (x/U_0). We have sketched $\tau(x)$ for the three possible signs of V_0 in Figure 4a. These results suggest that there will be an enhanced spatial decay rate of larval density in the regions where the flow is offshore.

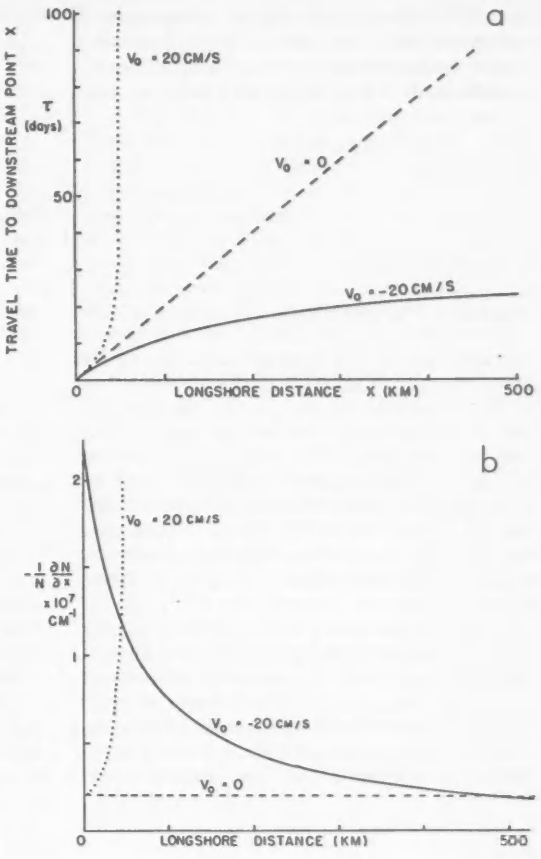

FIGURE 4.—a) The travel time τ necessary for larvae to reach the point x down the shelf from the spawning site at x = 0. The values of τ are computed in the absence of an eddy ($V_0 = 0$) and when an eddy induces onshore ($V_0 = -20$ cm/s) and offshore ($V_0 = 20$ cm/s) flows. b) The rate of change in numbers of larvae N with distance down the shelf x, plotted against longshore position for the three values of V_0.

When the flow is onshore ($V_0 < 0$) we can also solve Equations (8) and (9) and find

$$N(x,t) = N_0(t - \tau)\frac{U_0}{U(x)}e^{-\mu\tau}. \tag{14}$$

In this case, the timelike variable τ increases less rapidly with x than in the base case. This alone would lead to a slower spatial decay; however, the dilution effect (the U_0/U factor) counters this. In most cases, the dilution will be stronger than the effects of decreased transit time.

Perhaps the simplest way to see this is to consider the downstream decay rates when the source of larvae is constant in time and the onshore or offshore flows are spatially uniform. The spatial decay rates $-(\partial N/\partial x)/N$ for the three flow cases are

$$-\frac{1}{N}\frac{\partial N}{\partial x} = \begin{cases} \dfrac{\mu}{U_0} & \text{for } V_0 = 0 \\ \dfrac{\mu}{U} & \text{for } V_0 > 0 \\ \dfrac{\mu}{U} + \dfrac{1}{U}\dfrac{\partial U}{\partial x} & \text{for } V_0 < 0. \end{cases} \tag{15}$$

We have plotted these as functions of x in Figure 4b using $\mu = 10^{-7}$ s^{-1}, $U_0 = 5$ cm/s, $V_0 = \pm 20$ cm/s, and $Y = 200$ km. With this value for μ, two-thirds of the larvae disappear from the population because of the various biological causes within 4 mo from hatching. Most values of μ in the literature (e.g., Sissenwine et al. 1983) tend to be higher (see, however, Peterson

and Wroblewski 1984), but it is important to remember that these also include the advective losses. We have therefore chosen a smaller value of μ to reflect only biological processes; alternate values of μ will be considered shortly. The graph shows the extreme situation where the inflow or outflow is uniform over the whole downstream distance. The decay rate with distance travelled is always increased for offshore flow. For onshore flow, the decay rate can be reduced below the "no-ring" case but only very far downstream ($x > 500$ km) where the flow rate down the shelf is huge ($U = 30$ cm/s). Since onshore flows of 20 cm/s over a 500 km stretch of shelf are not likely to occur, we can conclude that the spatial decay rate will be enhanced in both the regions of onshore flow and the areas with offshore flow.

The net result, when a stream of larvae moving down the shelf and declining in density due to biological losses encounters a stationary eddy, can be calculated by combining the result for offshore flow in the region $0 < x < D$ with the one for onshore flow in $x > D$ where the ring is centered at the point $x = D$. In Figure 5 we compare the solution without the eddy

$$\frac{N}{N_0} = \exp\left(\frac{-\mu x}{U_0}\right) \tag{16}$$

to that with the eddy

$$\frac{N}{N_0} = \begin{cases} \exp(-\mu\tau) & \text{for } 0 < x < D \\ \dfrac{U(D)}{U(x)} \exp(-\mu\tau) & \text{for } D < x < W \end{cases}, \quad \tau = \int_0^x \frac{dx'}{U(x')} \tag{17}$$

where W is the length of the shelf domain, taken to be 500 km. Most of the decrease in population density occurs in the onshore flow regime; the final density is only half of that which would occur in the absence of the eddy. In assessing the causes of the population decrease, it is clear that the physics and the biology play comparable roles: the decrease in density when there is no eddy is a factor of two during the transit down the shelf (Fig. 5). The changes in density which occur predominantly in the region of onshore flow when the currents are present, give another factor of 2.5 decrease. Note that recruitment cannot be inferred directly from these density patterns; we will address the implications for recruitment in the section on Moving Eddies below.

We summarize the impact of stationary rings for various values of the onshore-offshore flow rates and the scale length along the shelf impacted in Figure 6. Here we plot contours of the ratio of the population density far downstream of the eddy (N_∞) to that

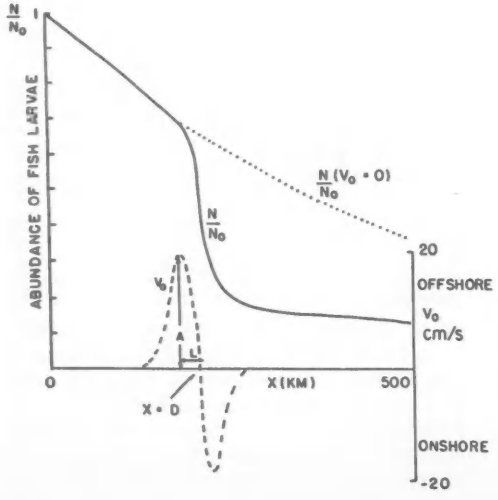

FIGURE 5. – Same as Figure 3 except biological losses ($\mu = 10^{-7}$ s^{-1}) are included.

which would be present without any cross-shelf currents (N_∞, $V_0 = 0$). This figure shows clearly the increasing impact with stronger transports onto or off of the shelf edge. There are slight differences in this ratio if the biological decay is ignored and if the cross-shelf flows occur over large distances, since the longshore flow slows down significantly. We should note that the decrease in larval fish density compared with the no-ring case depends on two nondimensional parameters $P_0 = AL/U_0Y$ and $P_1 = \mu L/U_0$. Thus for values of μ, U_0, or Y other than 10^{-7} s^{-1}, 5 cm/s, and 200 km, the graph can be read with suitable values of A and L to give the desired values for these two nondimensional numbers:

$$L_{\text{graph}} = P_1 \times 500 \text{ km} = \frac{\mu L}{U_0} \times 500 \text{ km}$$

$$A_{\text{graph}} = \frac{P_0}{P_1} \times 2 \text{ cm/s} = \frac{A}{\mu Y} \times 2 \text{ cm/s}.$$

MOVING EDDIES

In the previous examples, we have considered the changes in fish larvae distributions which occur when the shelf water flows by a stationary eddy. But rings frequently translate to the southwest, following a track between the continental slope and the Gulf Stream. The translational speeds vary considerably, ranging from a few cm/s to perhaps 10 cm/s. This along-shelf ring movement has a profound influence on the ring's contribution to decreasing the concentration of larvae – in some cases, they may be swept offshore in the entrainment flow of a slowly translating ring; in other cases the ring may catch up to, dilute, and pass the organisms. Finally, if the ring and shelf water are moving at the same rate, the larvae may never experience the impact of the ring, or alternatively may be in a region under constant influence.

The physical effects of a moving ring upon the larval fish population can be estimated readily from the previous results; it is only necessary to remember that the important quantity is the rate at which the shelf water moves relative to the eddy. If the ring is propagating westward more slowly than the westward drift of the shelf water, the organisms are in contact with the ring for longer periods of time, corresponding to a decreased value for the effective current U_0. But decreasing the effective downstream flow rate while keeping the eddy size constant is equivalent to increasing the length scale of the shelf region influenced by the ring's cross-shelf flows while the longshore current speed is maintained. Figure 6 shows clearly that such an increase in L will cause a greater reduction in larval density downstream of the eddy. As the eddy translation rate becomes closer and closer to the flow rate on the shelf (effectively increasing L in Figure 6), the effect upon the population becomes larger and larger, until eventually the eddy is drawing all of the larvae off the shelf as it passes. This occurs when the ring's speed is great enough so that the longshore transport of water relative to the ring is smaller than the offshore transport induced by the currents at the shelf edge:

$$U_0 - c < \int_0^x \frac{V_0(x')}{Y}\, dx' \qquad (18)$$

where c is the speed of translation of the ring.

If the ring is moving faster than the shelf currents, the situation is somewhat different; now the eddy catches up to the larvae and they are first influenced by a region of onshore flows and then by offshore currents. We can calculate the impact upon the population using the same methods as were employed in deriving Equation (10). For simplicity, we consider a domain which is infinite in x and compare the population density in regions which have not felt the ring with that in regions which have passed through the ring. For a ring moving at speed c, the equations describing the effects of the currents upon the population are

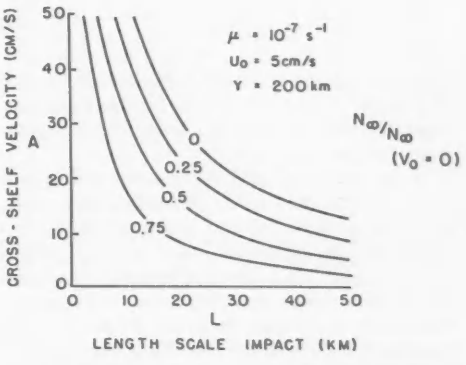

FIGURE 6. – The ratio of the number of larvae present far downstream of the eddy N_∞ to the number present if there were no eddy, $N_\infty(V_0 = 0)$. Contours of the ratio are plotted for different values of eddy size (L) and cross-shelf velocity A.

$$\frac{\partial}{\partial x}\left[(U-c)N\right] = \begin{cases} -V_0\dfrac{N}{Y} & \text{for } V_0 > 0 \\ 0 & \text{for } V_0 < 0 \end{cases} \qquad (19)$$

$$\frac{\partial U}{\partial x} = -\frac{V_0}{Y}$$

and the population change caused by the eddy when the downstream flow is sufficiently faster than the ring's translation rate is

$$\frac{N(\infty) - N(-\infty)}{N(-\infty)} = \frac{1}{Y}\int_{V_0>0} \frac{V_0(x,0)}{U_0 - c}\,dx,$$

$$c < U_0 - \frac{1}{Y}\int_{V_0>0} V_0\,dx. \qquad (20)$$

When the flow stagnates relative to the ring at some point, we have

$$N(\infty) = 0 \qquad U_0 - \frac{1}{Y}\int_{V_0>0} V_0\,dx < c < U_0 \qquad (21)$$

and when the ring is moving faster than the shelf waters

$$\frac{N(-\infty) - N(\infty)}{N(\infty)} = \frac{\dfrac{1}{Y}\displaystyle\int_{V_0>0} V_0\,dx}{c - U_0 + \dfrac{1}{Y}\displaystyle\int_{V_0>0} V_0\,dx}$$

$$c > U_0. \qquad (22)$$

These are plotted in Figure 7. Notice that the ring may cause substantial losses in the population, especially when its speed is roughly matched to the mean flow on the shelf.

In principle, one could write down an analytical solution to the full problem (Equations (8) and (9)), including a translating ring and a time-dependent source at the upstream edge of the domain. However, this is a rather cumbersome calculation, and we have chosen instead to solve these equations numerically and simply present representative pictures here of the ring induced effects when a cohort – a single patch of larvae spawned roughly simultaneously – moves down the shelf and is disturbed by a ring. Some care is necessary in selecting a numerical scheme, since centered differencing is unstable while upstream differencing introduces a numerical diffusivity (Roache 1972). This may not be undesirable, since in reality one would expect some mixing to occur along the shelf; but unfortunately the diffusivity is spatially variable, being lowest in the vicinity of the eddy, and this we do not want in the model. We compromised by choosing a very small grid scale (5 km) so that the effective diffusivity is only 1.2×10^6 cm^2/s. This is not completely negligible, as shown in Figure 8a which plots successive snapshots of the larval fish density at 15-d intervals in the absence of any rings (the time step was one-half day). The population at the beginning of the domain is assumed to enter in a pulse

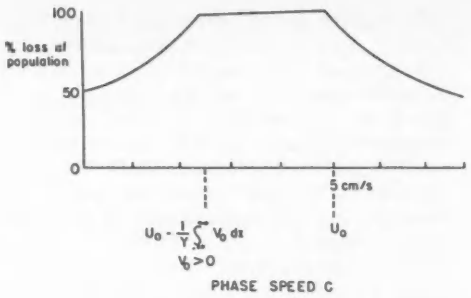

FIGURE 7. – Percent of the total number of larvae produced at the spawning site which are ultimately lost when a moving eddy is present at the shelf edge. When the speed c of the eddy is greater than $U_0 - 1/Y \int^x V_0$, all the larvae advected along the shelf are drawn offshore. When the ring is moving faster than the down-shelf current U_0, the ring catches up to the larvae, which are then diluted before being drawn offshore.

$$N_0(t) = \exp\left[-\frac{1}{2}\left(\frac{t}{5\text{ d}}\right)^2\right]. \qquad (23)$$

The gradual decrease in the peak abundance and the spread in width is caused by the numerical diffusion. Also included in this figure are the simple cases adding biological decay (Fig. 8b), a stationary ring (Fig. 8c), or both simultaneously (Fig. 8d). Note the large decreases in density induced as the population passes the ring and also the slower advection of the population down the shelf so that the organisms downstream are half a month older than they would otherwise have been (compare Figure 8b and 8d).

Finally, we show in Figure 9 two cases when a moving ring interacts with a patch of larvae. In the first case, the eddy is moving at 7 cm/s (faster than the 5 cm/s drift rate of the shelf water), so that the eddy catches up to the population and passes by it.

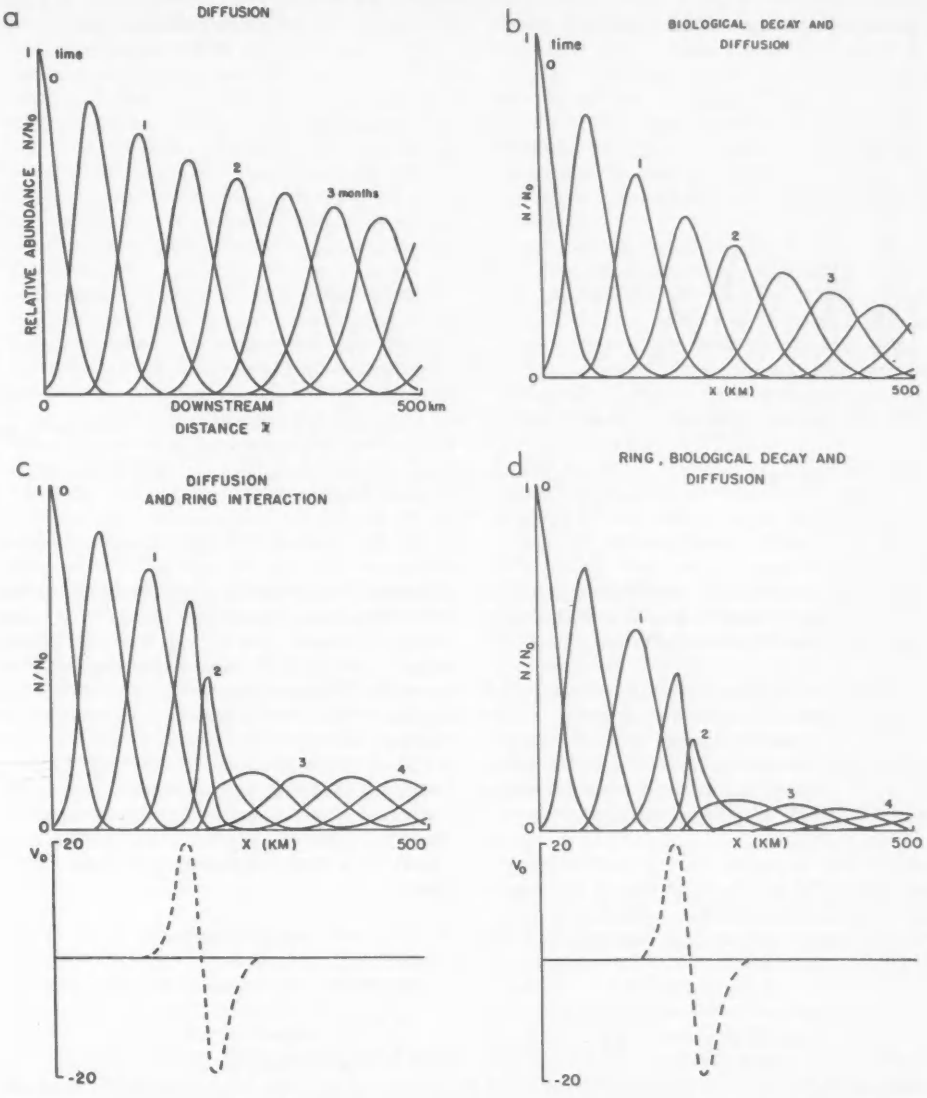

FIGURE 8. – Time-dependent solution of the numerical model which includes a) the diffusion of a spawning group or cohort of larvae as the patch is advected down the shelf. Snapshots are at 15-d intervals. Parameters $\mu = 0$, $U_0 = 5$ cm/s, $\Delta x = 5$ km, and $\Delta t = 0.5$ d. b) Same as (a) except $\mu = 10^{-7}\ s^{-1}$. c) Same as (a) except a stationary ring is present at the shelf edge, with parameters A = 20 cm/s and L = 20 km. d) Same as (c) except $\mu = 10^{-7}\ s^{-1}$.

As the ring passes by, the patch of larvae is spread out and distorted. Some losses do occur, but because of the rapidity of the interaction, these are slight. Comparison of this picture with Figure 8d shows that the larval density at 4 mo is higher than that for the stationary ring case. On the other hand, in the case when the shelf flow is faster than the speed of the ring (Fig. 9b), the impact of the ring is tremen-

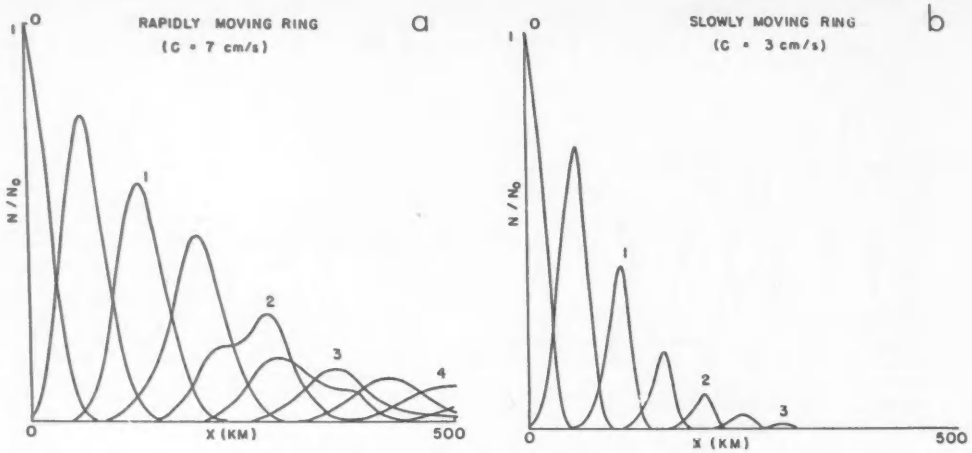

Figure 9.—a) Same as Figure 8d except a moving ring is present at the shelf edge, with parameters A = 20 cm/s, L = 20 km, and c = 7 cm/s. b) Same as (a) except c = 3 cm/s.

dous. When the population catches up to the back side of the eddy, the relative speed is so slight that all of the organisms are diverted off the shelf and lost from the system.

In addition to the plots of density versus time and along-shelf distance, it is extremely useful to consider the net balances for larvae within the domain. By integrating Equation (8) over x and t, using Equation (9) to evaluate the starting point contribution at $x = 0$, we can calculate the percentages of the total incoming population which are removed from the domain by three processes. First, there are biological decreases of the net population (due to the integrated μN term). It is important at this point to recall that we consider this as representing both larval death and metamorphosis. Therefore the recruitment should be roughly proportional to this term. (We do not consider the development time history of the larvae here; clearly this model could be combined with more detailed and complex larval development models to attempt more sophisticated recruitment predictions.) Secondly, there are losses due to advection off the shelf by the ring currents, and thirdly, larvae can be lost out the downstream end of the domain. The 500 km length of the domain puts the end of the model region near Cape May; exiting larvae may be swept offshore into the Gulf Stream and, like those drawn off by ring currents, presumably be lost.

The magnitude of each of these terms is summarized in Table 1 for the cases plotted in Figures 8b, d and 9a, b. Table 1 shows that the ring-induced advective losses from the population can be as large as or larger than the biological (mortality and metamorphosis) losses. This is most dramatic when the ring is moving slightly slower than the shelf water currents. The recruitment should vary in a fashion similar to the integrated biological causes term in Table 1; thus we expect a strong year class when rings are not interacting with the shelf waters, a reduction when stationary or rapidly moving rings are present, and a very sharp decrease in recruitment if a slowly moving ring is near the edge of the shelf at the time of spawning and larval development.

DISCUSSION

Theoretically, the passage of warm core rings close

TABLE 1.—Percent of total larval fish population entering the domain. WCR = warm core ring.

In the presence of	Biological causes	Advection off the shelf in flows induced by a WCR	Advection out of the downstream end of the domain
No ring $\mu = 10^{-7}\ s^{-1}$	62	—	38
Stationary ring A = 20 cm/s L = 20 km	42	46	12
Rapidly moving ring c = 7 cm/s	54	29	17
Slowly moving ring c = 3 cm/s	18	82	0

to the continental shelf should have considerable influence on the abundance and distribution of shelf-water larval fish and consequently on their recruitment to the fishery. Our simple mathematical model suggests a major effect of the ring-induced cross-shelf flows is to cause decreases in the larval density ahead of the ring where there is onshore flow. In addition, water being drawn off the shelf in an entrainment feature behind the eddy can carry larvae away, constituting a significant loss to the shelf population.

Research scientists of the National Marine Fisheries Service are currently investigating the frequency of entrainment events and their impact upon the fisheries (A. Friedlander[3]). Here we shall briefly examine the published literature on ring distributions and larval fish surveys. We have used the schematic charts of sea surface temperature produced by NOAA and ONR (Office of Naval Research). All of these records are necessarily incomplete due to cloudiness in the imagery and the difficulties in inferring water motions from the surface features. We therefore will make a somewhat subjective estimate of ring importance by considering the persistence of various eddies and their closeness to the shelf.

Figure 10 is a composite of the observed MARMAP distributions of cod *Gadus morhua*, larvae in the shelf region near Georges Bank during the late winter and spring of 1977 (Smith et al. 1979). We have placed on this figure the approximate locations of the warm core rings shown on the Experimental Ocean Frontal Analysis Chart produced by the U.S. Naval Oceanographic Office for this period. Figure 11 shows the corresponding MARMAP distributions for haddock, *Melanogrammus aeglefinus*, larvae.

Four warm core rings had trajectory paths near enough to Georges Bank during the spring spawning period in early 1977 to have had significant impact upon the larval fish distributions according to the predictions of our model. In front of each ring shown on Figures 10 and 11, the concentration of larvae over the shelf appears to be relatively low, much as our model suggests would occur in areas of ring-induced onshore flow. There even appear to be indications of entrainment of larvae off the shelf behind rings 77E (Figs. 10c, 11c) and 77A (Fig. 11d). Unfortunately the MARMAP station grid does not extend beyond the 200 m contour, so that this cannot be confirmed from the historical data. Extending the MARMAP grid further offshore would be of great benefit in assessing losses of larvae both by rings and by other offshore transports. It is also not possible to differentiate between patchiness from concentrated spawning upon Georges Bank or other biological causes and ring-induced variations. Again this makes the relationship between theory and data difficult to assess.

Warm core ring 77A (Figs. 10, 11) is an example of a nearly stationary eddy, remaining adjacent to Georges Bank from 30 March to 25 May 1977. But according to our theory, ring 77E is potentially even more dangerous, since it slowly sweeps down the entire Georges Bank edge between 18 May and 6 July, moving at 3-5 cm/s. Drifting groups of larvae could have caught up to the back side of ring 77E and been drawn off the shelf.

The survival of larvae in 1977 was low, and the year class was weak for both cod and haddock (Serchuk and Wood 1981; Clark et al. 1982). In other years also, there appears to be a relationship between the frequency of ring interaction with Georges Bank during the winter and spring spawning season and subsequent year-class strength for both cod and haddock stocks (Table 2). Cod spawn on Georges Bank from December into May and haddock spawn from February into June (Smith et al. 1979). Therefore we have examined the 6-mo period from January to June each year from 1975 to 1979 for ring activity using the charts of Bisagni (1976), Mizenko and Chamberlin (1979a, b), Celone and Chamberlin (1980), and Fitzgerald and Chamberlin

TABLE 2.—Apparent relationship between years of less frequent WCR (warm core ring) interaction with Georges Bank during the winter and spring spawning season and strong recruitment of cod and haddock stocks.

Year	Recruitment Strength		No. of WCR's interacting during spawning season (Jan.-June)	Comments
	Cod	Haddock		
1975	Very good	Very good	1	Eddy 6 present February-April
1976	Weak	Weak	3	WCR 75I, 76A, and 76C detrimental; 76D too far offshore
1977	Weak	Weak	4	WCR 76F, 76G, 77A, and 77E all detrimental
1978	Good	Very good	1	WCR 78A present in May; 78B too far offshore
1979	Weak	Average	3	WCR 78I, 79A, and 79B detrimental

[3]A. Friedlander, Northwest Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, R.R. 7A, Box 522A, Narragansett, RI 02882, pers. commun. January 1983.

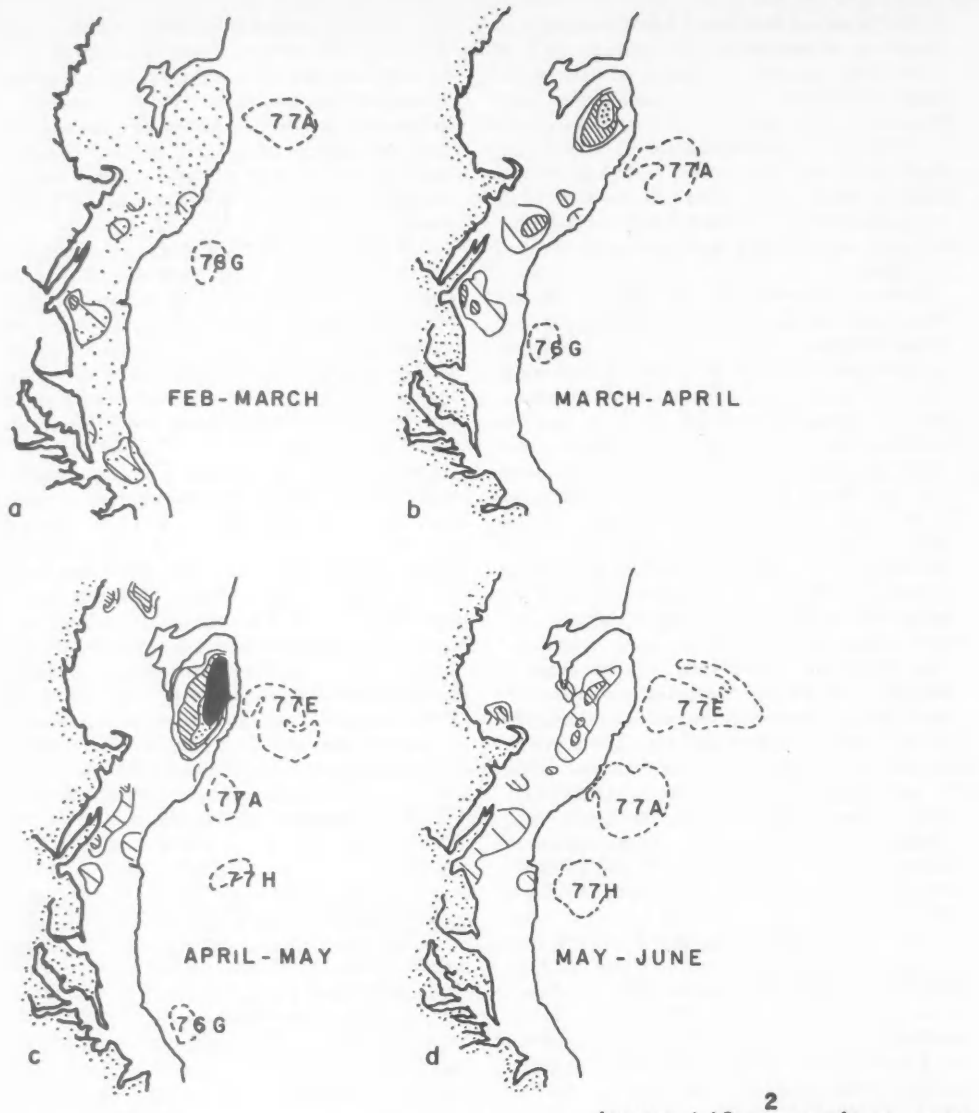

FIGURE 10.—Distribution and abundance of Atlantic cod, *Gadus morhua*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The solid outline of the bottom topography is the 200 m contour. The positions of warm core rings 76G, 77A, 77E, and 77H are replotted from Experimental Ocean Frontal Analysis Charts produced by the U.S. Naval Oceanographic Office on 25 February (a), 23 March (b), 27 April (c), and 25 May (d) in 1977. The dots on (10a) show the sampling locations.

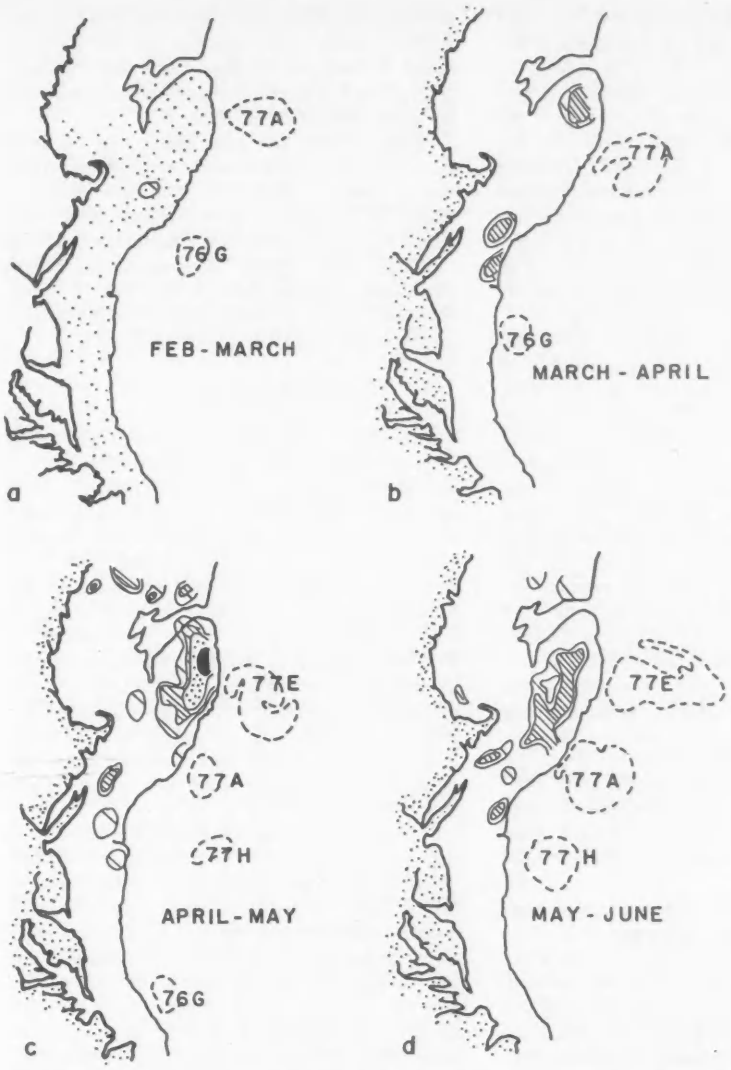

FIGURE 11. – Distribution and abundance of Atlantic haddock, *Melanogrammus aeglefinus*, larvae off the eastern United States during the latter part of the 1976-77 spawning season (redrawn from Smith et al. 1979). The positions of the warm core rings are the same as in Figure 10.

(1981). The number of rings present in the Slope Water is less important than the trajectories of the rings. If they pass too far offshore or appear too early or too late in the spawning season, they may have little impact. It is difficult to measure the magnitude of the onshore-offshore flows from the remote sensing data, but we have tried to consider the size of the shelf edge affected and the longshore speed of the eddy when judging the strength of a particular interaction. Unfortunately, we have no information for the years considered on the timing or location of spawning which undoubtably is important in determining the impact of individual rings.

The spring of 1975 was a time of low warm core ring activity (Table 2), and both cod and haddock produced good year classes, essentially the best since the 1960's (Smith et al. 1979). This high recruitment was not due to large numbers of larvae being spawned; indeed, the abundance of cod and haddock larvae was at a 5-yr low (Smith et al. 1979). Apparently, the few larvae present on Georges Bank experienced exceptionally high survival. There was only one ring (designated eddy 6 by Bisagni 1976) which by our model predictions could have influenced recruitment. Eddy 6 was in the vicinity of Georges Bank from February through April but did not seem to be entraining shelf water for this entire period.

During the spring of 1976 there were three, possibly four, warm core rings interacting with Georges Bank between January and May. Mizenko and Chamberlin (1979a) presented the track lines for eddies 75I (which later possibly became 76B), 76A, and 76C. Rings with these trajectories had the potential to affect recruitment. The 1976 year class strength for both cod and haddock stocks was weak (Smith et al. 1979).

The spring of 1977 was a year of unusually high ring activity. Figure 1 shows five rings (77A, 77C, 77E, 77G, and 77H) simultaneously present in the Slope Water region on 11 May 1977. Mizenko and Chamberlin (1979b) presented trajectories for all the eddies observed in 1977. Of these rings, 76F, 76G, 77A, and 77E appear to be most detrimental. The 1977 year-class strength for both cod and haddock stocks was again weak (Serchuk and Wood 1981; Clark et al. 1982).

The relationship of low ring activity and high recruitment observed in 1975 holds true again for 1978. This was a good year for cod and a very good year for haddock recruitment (Serchuk and Wood 1981; Clark et al. 1982). Examining the trajectories of warm core rings present during 1978 (Celone and Chamberlin 1980), we find no rings interacting with Georges Bank until late May or June. During the 60-d period from mid-February to mid-April, no anticyclonic eddies were apparent off the northeast coast. In late April and May, there were two rings (78A and 78B), but they occurred too far south or too far offshore to affect the Bank.

Finally in 1979, the most recent year for which there are both fisheries recruitment data and trajectory records, we find three potentially dangerous rings: 78I, impinging upon Georges Bank from March to July (Fitzgerald and Chamberlin 1981) and two eddies, 79A and 79B, lingering southwest of the Bank from February through May. The 1979 year class was weak for cod and only average for haddock (Serchuk and Wood 1981; Clark et al. 1982).

CRITIQUE

According to our calculations, warm core rings may have considerable influence on the distribution and ultimate survival of cod and haddock larvae spawned on Georges Bank. Our simple mathematical model demonstrates the possible effects of cross-shelf flows induced by a ring upon larval fish distributions and abundance. The ring's size, strength, and translation speed are critical in determining its potential impact. A stationary ring may cause a 20 to 50% loss of larvae by inducing advective transport off the shelf. If a ring is moving, the impact can be even greater, especially for an eddy travelling longshore at a slightly slower speed than the shelf water. In this most catastrophic case, a group of larvae can catch up to the back side of the eddy and be entirely swept off the shelf.

In briefly examining the published literature on ring trajectories and fisheries recruitment statistics, we have found what appears to be a relationship between years of frequent ring interaction with Georges Bank during the late winter and early spring spawning season and weak year classes of cod and haddock. Our analysis can be criticized as cursory and incomplete since we had no detailed information on entrainment features or on many important biological factors such as the timing and location of spawning. Future studies may show this relationship was fortuitous; however, our results certainly indicate that future study is warranted.

An implicit assumption in our analysis of ring events and fisheries recruitment data is that advective losses can affect year-class success. This has not yet been demonstrated for the Northwest Atlantic; however, Parrish et al. (1981) presented convincing arguments that the dominant exploitable fishes off the west coast have adopted spawning behaviors which minimize losses due to offshore transport.

They suggested that deviations from normal transport conditions may be a cause of the very large recruitment variations observed in the fisheries for sardine and anchovy. Whether warm core rings represent anomalous conditions or whether the shelf fishes of the Northwest Atlantic have adopted spawning patterns which minimize the losses by entrainment is yet to be discovered.

G. Laurence[4] has suggested that in some instances vertical migratory behavior may prevent significant numbers of larvae from being advected offshore. If the entrainment feature is shallow and the fish larvae avoid the surface layer, then the offshore transport could be much less than predicted by our model. The National Marine Fisheries Service is currently surveying entrainment features associated with warm core rings to assess the losses occurring off the shelf. Recently, Wroblewski and Cheney (1984) reported finding significant numbers of the white hake, *Urophycis tenuis*, larvae 140 km seaward of the Scotian Shelf break in Slope Water which had been entrained by a warm core ring. *Urophycis tenuis* spawn on the Scotian Shelf and upper continental slope. Wroblewski and Cheney concluded that the ring altered the usual larval drift pattern along the shelf edge. Curiously, no larvae of cod or haddock, which also spawn on the shelf during spring and summer, were found in the ichthyoplankton net tows. It remains to be demonstrated whether sufficient numbers of shelf-spawned larvae are transported offshore by rings to affect recruitment of shelf stocks.

The advective losses predicted by our model may be overestimates if only larvae present near the shelf edge are susceptible to entrainment and if their density is much lower than that further inshore. The influence of the ring may not reach the shallower regions where many larvae are found. Also, biological losses may be larger than assumed in the model, so that the relative importance of ring-induced losses may be less.

Warm core ring entrainments are not the sole mechanism by which fish larvae can be transported off the shelf. In 1955, Chase found a relationship between haddock recruitment and the strength of the wind-driven current normal to the southern side of Georges Bank. We also recognize that there could even be beneficial effects to the Georges Bank ecosystem if the ring-induced cross-shelf flows push nutrient-rich Slope Water onto the Bank and fertilize the system (G. A. Riley[5]). Rather than exploring all mechanisms, we have chosen to assess one particular source of variability which may contribute to fluctuations in year-class strength for the fish stocks spawning on Georges Bank.

We have also assumed that the fish larvae are well mixed across the shelf, although we know that they are generally distributed in patches. Thus our model solutions may be comparable with field data only if one integrates the field data over x and z as we have done in our simplified model. Fisheries recruitment data naturally reflects this integration over large spatial scales and we are encouraged by the apparent relationships in Table 2. However, loss during the larval period is only one factor affecting recruitment. Events during the postlarval stages are also significant; Sissenwine et al. (1983) showed that predation in these later stages is an important factor in year class success.

Our model has given quantitative but crude estimates of the importance of ring events for larval survival and suggested that the impact of the ring depends strongly upon its motion; investigations with more highly resolved and more complex models and further survey work for assessing both ring and mesoscale eddy influences on larval fish distributions and subsequent recruitment are the next steps.

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FIELD AND LABORATORY ASSESSMENT OF PATTERNS IN FECUNDITY OF A MULTIPLE SPAWNING FISH: THE ATLANTIC SILVERSIDE *MENIDIA MENIDIA*[1]

DAVID O. CONOVER[2]

ABSTRACT

Patterns in fecundity (i.e., spawning frequency, batch fecundity, annual egg production) of a multiple spawning fish, the Atlantic silverside, *Menidia menidia*, were assessed by 1) gonadal analysis of field specimens, 2) visual observations of spawning periodicity in the field, and 3) laboratory experiments. The gonadal analysis assumed that the difference between total number of eggs (recruitment + mature) per female just prior to the beginning of spawning, and recruitment egg retention per female at the end of the spawning season, represented annual egg production. Annual egg production estimated in this manner was 893 ± 197 eggs/g ovary-free body weight (±95% C.L.). Batch fecundity (no. eggs in the most advanced size class/g ovary-free body weight, ±95% C.L.) varied significantly during the breeding season, being lowest near the beginning (179 ± 21) and end (181 ± 28), and highest during the middle (266 ± 34 and 267 ± 23) of the breeding season. Batch fecundity averaged over the entire breeding season, was about 225 eggs/g ovary-free body weight, indicating that each female must spawn about four times. The gonadal estimate was tested by inferring the actual spawning frequency from daily, visual observations of spawning in the field. These observations showed that spawning occurred on a fortnightly cycle coincidental with new and full moons, and that each female spawned at most once per semilunar period. There were about four semilunar spawning phases during the breeding season, indicating close correspondence with the results of gonadal analysis.

Laboratory observations demonstrated that female *M. menidia* are physiologically capable of spawning more frequently than in nature. Total egg output in the laboratory was about twice that in the field.

Accurate estimates of fecundity are important in describing the dynamics of fish populations. In some fishes, all eggs mature synchronously and are shed in a single batch over a relatively brief period of time each year (Bagenal 1967). Estimating fecundity in such species is a simple process of enumerating the number of ripening eggs per female. However, in many other fishes, ova mature in multiple batches that are spawned successively within one spawning season. These species have been termed multiple spawners, batch spawners, serial spawners, or fractional spawners by various authors (Bagenal and Braum 1971; Hempel 1979; DeMartini and Fountain 1981; Gale 1983; Snyder 1983). Little is known about the patterns in fecundity of multiple spawners, even though many marine and freshwater fishes from diverse taxonomic groups in both temperate and tropical regions produce eggs in this manner. Determination of annual egg production in multiple spawners is difficult and recent studies have indicated that in some species, previous assessments may be in error by as much as an order of magnitude (Hunter and Goldberg 1980; Hunter and Leong 1981; DeMartini and Fountain 1981).

Frequency distributions of egg size (diameter) within ovaries of multiple spawning fishes are characteristically multimodal (Hempel 1979). In most multiple spawners, a synchronously maturing batch of eggs that is accumulating yolk sequentially arises from a much larger group of previtellogenic immature eggs, termed "recruitment" ova (Clark 1925; Bagenal and Braum 1971; Jones 1978; Hunter and Leong 1981). The problem in estimating fecundity has been to determine how many modes or batches of eggs are spawned annually. The conventional approach has been to count only the largest eggs or those above an arbitrary size (e.g., all yolked eggs) under the assumption that smaller eggs would be resorbed or spawned in later years. Whenever this assumption is incorrect, fecundity can be grossly underestimated. A second approach has been to infer the spawning frequency of adults from the proportion of field-collected females in ready-to-spawn condition (i.e., those containing hydrated eggs, e.g., Demartini and Fountain 1981) or from females showing evidence of having just spawned (i.e.,

[1]Contribution No. 89 of the Massachusetts Cooperative Fishery Research Unit, University of Massachusetts, Amherst, MA, and Contribution No. 437 of the Marine Sciences Research Center, State University of New York, Stony Brook, NY.

[2]Marine Sciences Research Center, State University of New York, Stony Brook, Long Island, NY 11794.

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presence of 1-d-old postovulatory follicles, observed histologically, Hunter and Goldberg 1980). Spawning frequency is then multiplied by batch fecundity (number of eggs in the largest size class) to arrive at annual fecundity. Excellent examples of this methodology can be found in DeMartini and Fountain (1981), Hunter and Goldberg (1980), and Hunter and Macewicz (1980). A third technique for estimating fecundity in multiple spawners has been laboratory experiments where females are confined and allowed to spawn repeatedly (Gale and Gale 1977; Gale and Buynack 1978, 1982; Hislop et al. 1978; Gale 1983). The problem here is that spawning frequency and fecundity are dependent on the food supply (Wootton 1973, 1977, 1979; Townshend and Wootton 1984), so that it may be difficult to interpret laboratory data unless detailed studies of feeding rate and/or fecundity of fish in nature have been previously conducted (e.g., Hunter and Leong 1981).

The ovarian cycle of many fishes that breed during a restricted season involves two major, alternating phases of oocyte production and growth: 1) a previtellogenic phase during which new oocytes are produced, cell organelles form, and cytoplasmic growth occurs; and 2) a vitellogenic phase during which growth is faster and yolk accumulates in the ovum (Ball 1960; Jones 1978; Tokarz 1978; Baggerman 1980). The greatest production of new oocytes and phase one growth occurs during the postspawning season, with vitellogenic growth and maturation of eggs occurring just prior to and during the spawning season (this may not be true in tropical or other fishes that breed throughout most of the year, see reviews by Ball 1960; Jones 1978; Baggerman 1980). Hence, in multiple spawners having a restricted breeding season, the reservoir of recruitment eggs may be largely formed prior to the breeding season. If true, then the number of recruitment eggs per female should consistently decline as the breeding season progresses. The rate of decline in number of eggs per female would provide an estimate of seasonal egg production, and spawning frequency per female could be estimated from the total number of eggs shed divided by batch fecundity. The method could be tested by comparing the estimated spawning frequency with the actual spawning frequency determined independently in some other manner.

The purpose of this paper is to describe patterns of batch fecundity and annual egg production in the Atlantic silverside, *Menidia menidia*. The analysis employs the method described above: I show how the total number of eggs per female (recruitment + maturing) present at the beginning of the spawning season minus recruitment eggs per female retained at the end of breeding can be used as an estimate of total egg production. The method is tested by showing that predicted spawning frequency is identical to the spawning frequency inferred from direct visual observations of spawning periodicity in a field population. Observations of spawning frequency and egg production under laboratory conditions are used to demonstrate that individual females are physiologically capable of maintaining the egg production rates and spawning frequency estimated from field populations.

The Atlantic silverside, *Menidia menidia*, (Pisces: Atherinidae) is a multiple spawning marine fish that inhabits coastal waters of eastern North America (Middaugh 1981; Conover and Kynard 1984). *Menidia menidia* is an annual fish: all individuals mature at age 1 and < 1% of breeding populations are 2 yr old. The ecological importance of *M. menidia* in terms of biomass transport from salt marsh to offshore communities and as forage for piscivorous fishes has been previously documented (Bayliff 1950; Conover and Ross 1982; Conover and Murawski 1982). The Atlantic silverside is an excellent species for studying patterns in fecundity because it is numerous and can be easily collected, spawning is easy to visually observe in the field, and it readily breeds in the laboratory.

METHODS

Gonadal Analysis

Field Sampling

Fish were sampled from the salt marsh region of Essex Bay, MA, with beach seines. Specimens were collected every 2 wk during 1977 as part of a general study of the population ecology of *M. menidia*. Additional specimens were collected intermittently in the spring during the breeding season. All collections were made in daylight within 1-2 h of low tide, and all specimens were immediately preserved in 10% buffered Formalin[3]. Detailed descriptions of Essex Bay and sampling methodology are available in Conover and Ross (1982).

Fecundity

Gonads were excised and weighed (nearest 0.01 g) from fish captured on 11 dates from October 1976 to July 1977. All fish were measured for total length

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

(nearest millimeter) and gonad-free body weight (nearest 0.1 g). The gonadosomatic index (GSI) was calculated by expressing gonad weight as a percentage of total weight (Snyder 1983).

Preliminary microscopic examination of ripe ovaries from collections during the breeding season revealed three general egg types that corresponded with modes found in frequency distributions of egg diameters from ripe females (see Figure 1 below). The three egg classifications were defined by both size and appearance of the ova as follows:

Immature ova: spherical, 0.05-0.60 mm in diameter. The smaller ova in this group (0.05-0.15 mm) were primary oocytes with a clear cytoplasm and large nucleus. The larger ova (0.15-0.60 mm) were opaque and white. These ova formed one continuous mode in the frequency distribution so they were considered as one group (Fig. 1A, B).

Maturing ova: spherical, 0.6-1.0 mm in diameter, yellowish, and translucent.

Ripe ova: spherical, hydrated, 1.0-1.2 mm in diameter, hyaline and golden, with visible gelatinous threads coiled around the egg.

To confirm that these classifications represented distinct groups of synchronously maturing ova, I measured the diameter (random axis) of about 150 eggs, randomly subsampled from each of several females. In females captured during the breeding season, there were two distinct modes: the most advanced mode represented maturing eggs, and the other mode represented immature eggs (Fig. 1A). In females with ripe eggs, three modes in egg frequency were apparent: the most advanced group represented ripe eggs, the intermediate mode represented the next batch of maturing eggs, and the remaining mode consisted of immature eggs (Fig. 1B).

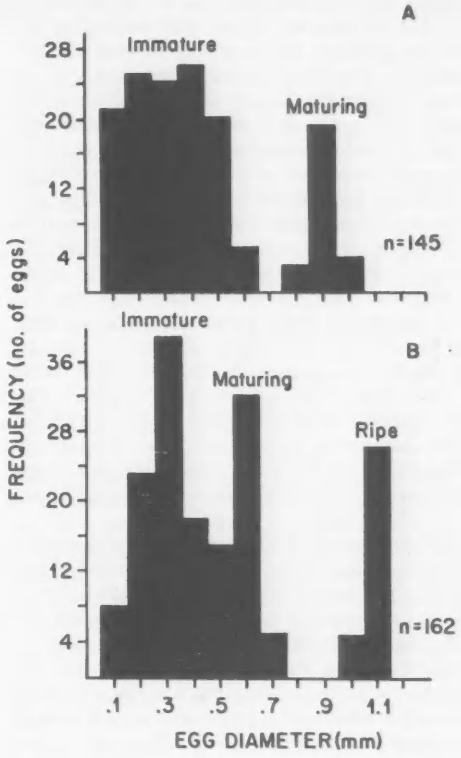

FIGURE 1.—Frequency vs. egg size (diameter in 0.1 mm intervals) for ova randomly sampled from two female *Menidia menidia* collected 6 June in Essex Bay, MA. A) A nonripe female in which there is a large number of immature eggs and a clearly definable mode of maturing eggs. B) A ripe female in which there is a large mode representing immature eggs, an intermediate mode of eggs beginning to mature, and an advanced mode of ripe eggs.

"Batch fecundity" was defined as the number of mature eggs in the most advanced size class, and presumably represented the number of eggs spawned at one time. As illustrated in Figure 1, the most advanced size class of maturing or ripe eggs was clearly distinguishable from, and did not overlap in size with, the immature ova. In ripe females, batch fecundity represented the number of hydrated eggs (e.g., the most advanced mode in Figure 1B). In nonripe females, batch fecundity represented the number of maturing eggs (e.g., the most advanced mode in Figure 1A). "Recruitment fecundity" was defined as the number of eggs smaller than the most advanced egg batch. Recruitment fecundity presumably represented the number of ova from which additional batches of mature eggs could potentially arise. In ripe fish containing three modes (e.g., Fig. 1B), the intermediate mode of eggs in early maturation was included with the immature eggs as part of the recruitment egg group because these overlapped in size with, and were difficult to separate from, immature ova. The minimum size of recruitment eggs was 0.05 mm in diameter. "Total fecundity" was defined as the sum of recruitment and batch fecundity.

Batch, recruitment, and total fecundity of individual females were estimated gravimetrically in the following manner. A cross section comprising 10-20% of the total ovarian weight was cut from a randomly chosen portion of one ovary. Both the sub-

sample and the remaining ovarian material were blotted on absorbent paper and weighed to the nearest milligram. The subsample was then placed in modified Gilson's fluid (Bagenal and Braum 1971), teased apart and vigorously shaken to separate ova, and stored for several weeks. All eggs in a subsample were counted and classified as belonging to either the recruitment pool or the mature batch of eggs. Batch and recruitment fecundities were then estimated for each female by multiplying the number of eggs in the subsample by an expansion factor (total ovarian weight/subsample weight). The mean diameter of the largest size class of eggs was also determined by measuring a random sample of about 20 mature eggs from each female. Shrinkage of eggs during preservation appeared to be minimal, so no correction for shrinkage was made. Fecundity was estimated for females collected on four occasions, from just before the beginning of the spawning season to its end. These dates were 6 May, 6 June, 22 June, and a pooled sample captured over the period 6-13 July.

To demonstrate whether estimates of fecundity were dependent on the location of the ovarian subsample, I compared these among replicate subsamples taken from the anterior and posterior sections of the right and left ovaries of six different females (i.e., four subsamples per female). Two-way ANOVA indicated that estimated fecundity was independent of subsample location ($P > 0.10$) and the coefficient of variation was low (CV = 4.2%). The ratio of the number of batch eggs to recruitment eggs was also independent of subsample location ($P > 0.5$). Moreover, I also directly counted the total number of batch eggs in four of the females used in the above analysis; in each case estimated batch fecundity was within 10% of the true value.

Field Observations of Spawning Frequency

The frequency of spawning in a natural population of *Menidia menidia* was inferred from daily, direct field observations of mating. The Atlantic silverside spawns in large groups of fish that broadcast milt and eggs amongst vegetation in the upper intertidal zone of salt marshes within 1 or 2 h of the daylight high tide (Middaugh 1981; Middaugh et al. 1981; Conover and Kynard 1984). At such times, spawning can be easily observed. My observations were conducted at a major spawning site in Salem Harbor, MA. Daily assessments of spawning intensity were conducted throughout the spawning season by counting the number of aggregations of spawning fish sighted during high tide. Methodological details are provided in Conover and Kynard (1984).

Laboratory Observations of Spawning Frequency and Egg Production

Spawning frequency and egg production were also assessed by confining fish in laboratory tanks. A summary of the experimental procedure, described fully in Conover and Kynard (1984), follows. A large group of *M. menidia* were captured at Salem Harbor on 5 May 1979 and transported to the University of Massachusetts marine laboratory at Gloucester, MA. One female and two male fish were placed into each of the four 74 L tanks at room temperature on a natural photoperiod. Four males and four females were also placed into each of two circular plastic pools (diameter 1.5 m, depth 0.3 m). These pools were located outdoors. All fish were fed fresh, chopped seaworms (*Nereis*) and amphipods in excess of daily consumption. Spawning substrates consisted of a small tuft of synthetic aquarium filter floss, anchored to the bottom of each tank or pool. The floss was checked several times daily for the presence of eggs. When eggs were discovered, the floss was replaced. All eggs were preserved and enumerated later. Eggs from each female were usually deposited in a distinct clump on the floss, providing a means for determining the number of females that had spawned in the previous interval. The experiment was allowed to continue until spawning ceased (27 July). Length and weight of spawners was measured at the conclusion of testing.

RESULTS AND DISCUSSION

Gonadal Analyses

In late fall, just prior to the offshore winter migration (Conover and Murawski 1982), ovaries represented about 1% of total body weight (Fig. 2) and contained only small (< 0.1 mm), clear, transparent eggs. Upon return of fish to the shore zone the following April, the ovarian GSI was about 4% and many opaque, white, immature ova (< 0.5 mm) were present. Of the 25 females captured on 6 May, 92% contained numerous immature ova and a clearly definable batch of maturing ova. The first female carrying ripe egges was collected on 12 May. The GSI peaked in both sexes on 25 May and declined thereafter until the end of July. The first fish in spent condition (no maturing egg class, recruitment eggs, if present, degenerating, GSI < 5%) was captured on 22 June. The proportion of spent fish was 23% on

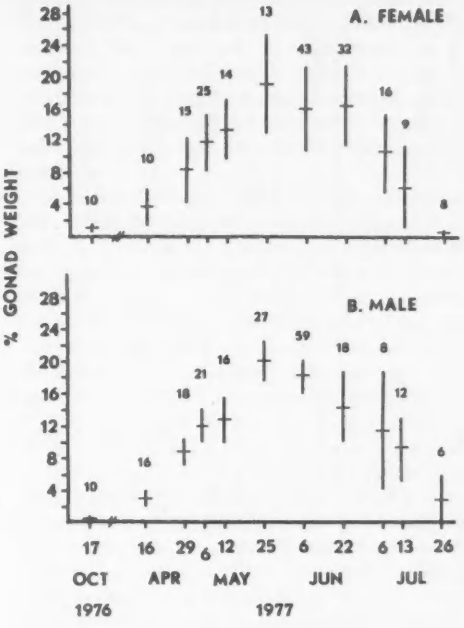

FIGURE 2.–Gonadosomatic index (gonad weight expressed as a percentage of total weight) for *Menidia menidia* collected during 1976-77 in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the sample size is given above the datum for each collection.

6-13 July and 100% on 26 July. Hence, the breeding season in Essex Bay began sometime after 6 May and was over by 26 July during 1977.

The potential annual fecundity of *M. menidia* may be represented by the total number of eggs (recruitment + maturing ova) within females just prior to the breeding season (i.e., 6 May), if additional immature eggs are not continually added to the recruitment pool as the spawning season progresses. If this premise is true, then there should be a continuous decline in recruitment fecundity and total fecundity during the breeding season (although not necessarily in batch fecundity).

Comparison of fecundities between sample dates was facilitated by the following observations. Total number of eggs per female was linearly related to ovary-free body weight (Fig. 3). Batch fecundity was also a simple linear function of ovary-free body weight (Fig. 4) and the rates of increase in batch fecundity, recruitment fecundity, and total fecundity with increase in female weight were generally similar among sample dates (i.e., regression slopes

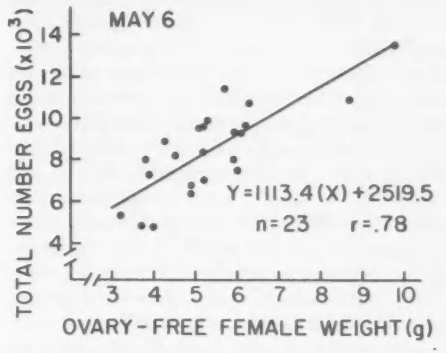

FIGURE 3.–Relation between total number of eggs (recruitment plus mature) and ovary-free female body weight for Atlantic silversides captured just prior to the beginning of the spawning season (6 May 1977) in Essex Bay, MA.

differed little, *t*-test, $P > 0.05$). Correspondingly, relative batch fecundity, relative recruitment fecundity, and relative total fecundity (relative fecundity = no. eggs/g ovary-free body weight) were each independent of body weight in nearly all tests (linear correlation, $P > 0.05$), suggesting that females of all sizes allocated about the same proportion of energy to reproduction. Hence, fecundity was adequately described and compared between dates if expressed as a proportion of ovary-free body weight, rather than as a function of weight.

Batch fecundity, recruitment fecundity, and total fecundity (no. eggs/g ovary-free body weight) during the spawning season are presented in Figure 5. Three patterns are evident. First, total fecundity and recruitment fecundity monotonically declined (Fig. 5A, B). Total fecundity was 1,609 ± 126 (95% C.L.) on 6 May and declined to 876 ± 177 by the second week of July (Fig. 5A) while recruitment fecundity was initially 1,430 ± 128 on 6 May and declined to 716 ± 164 in July (Fig. 5B). Second, batch fecundity differed significantly between sample dates, being maximal during the middle of the breeding season (266 ± 34 and 267 ± 23 on 6 and 22 June, respectively) and minimal at the beginning and end of the breeding season (179 ± 21 and 181 ± 28 on 6 May and 6-13 July, respectively; Fig. 5C). Third, many recruitment eggs remained in ovaries near the end of the spawning season (Fig. 5B) and most of these were probably resorbed soon thereafter because all females captured on 26 July contained only small (< 0.10 mm), transparent oocytes. Two females from the 6-13 July collection contained only immature eggs that appeared to be in a state of resorption and had no maturing egg group.

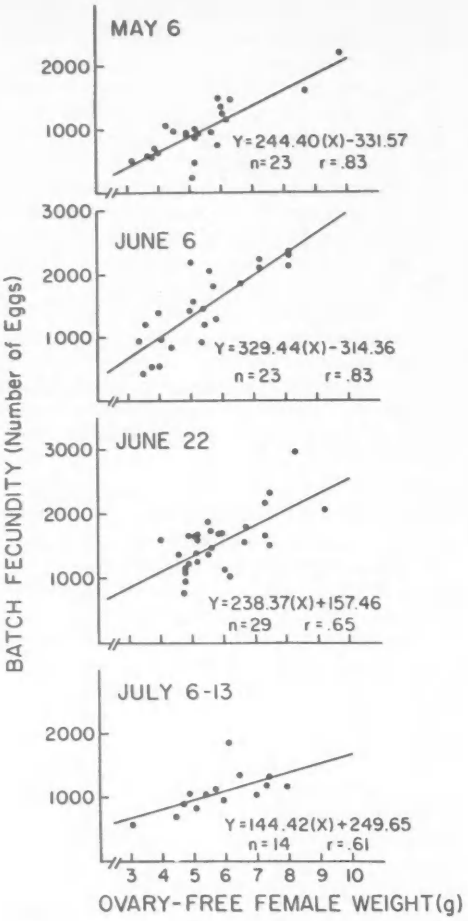

FIGURE 4.–Relation between batch fecundity (no. of eggs in the most advanced size class) and ovary-free female body weight for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA.

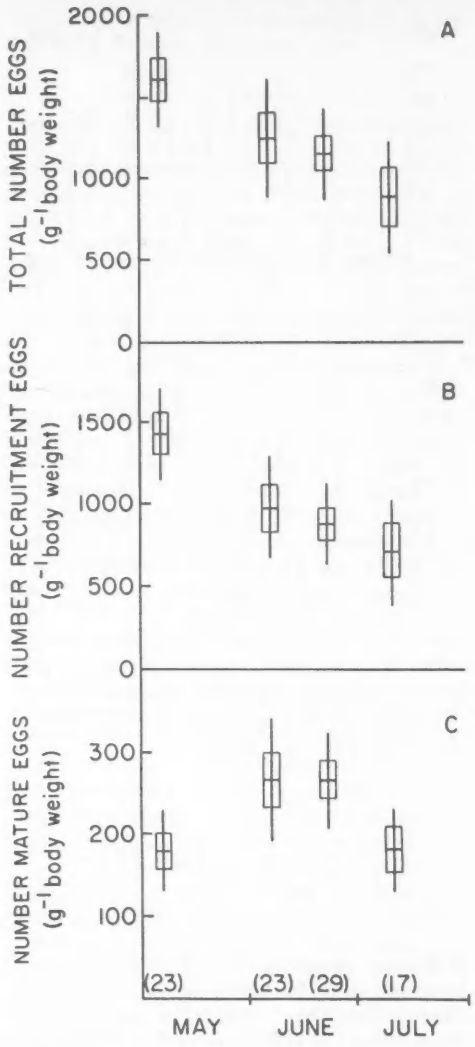

FIGURE 5.–Relative fecundity (no. eggs/g ovary-free female body weight) for Atlantic silversides captured on four occasions during the 1977 breeding season in Essex Bay, MA. The horizontal lines represent means, the vertical lines represent one standard deviation, and the rectangles represent 95% C.L. Sample sizes are in parentheses. All fish were spent on 26 July. A) Total number of eggs. B) Number of recruitment eggs (recruitment fecundity). C) Number of mature eggs (batch fecundity).

Batch fecundity as estimated above assumes that the number of eggs in the most advanced mode is not reduced by atresia as they grow and are eventually shed. I noted few eggs which appeared to be atretic or in a process of resorption (except near the very end of the breeding season) and females which had recently spawned usually contained few, if any, residual ripe eggs. Similar observations were reported by Clark (1925) for the atherinid *Leuresthes tenuis*. Moreover, if some eggs cease growing and are resorbed before reaching maturity, there should be a negative correlation between batch size and the mean diameter of eggs in the batch (i.e., no. batch eggs/g ovary-free body weight should generally be

lower in fish nearly ready to spawn than in fish where batch eggs are still maturing). Linear correlations of batch size and mean diameter of the maturing egg batch for each of the four dates on which fecundity was measured were nonsignificant ($P > 0.05$), suggesting that the number of eggs in a batch does not decline much as the oocytes grow to maturity.

Assuming that the recruitment pool of immature eggs is fully formed prior to the breeding season, an estimate of the actual number of eggs produced annually can be derived from the above data. Because recruitment eggs remain at the season's end, actual egg production is best represented by the total number of eggs present just prior to the beginning of the spawning season minus the number of recruitment eggs retained when the spawning season ends. For the above data, this provides a value of (1,609 ± 126) – (716 ± 164) = 893 ± 197 eggs/g ovary-free body weight (±95% C.L.). The mean body weight of females during the breeding season was 5.6 g so that the average female would have spawned about 5,001 eggs in a season. The mean batch fecundity over the spawning season was 223 eggs/g ovary-free body weight or about 1,249 eggs/female. Hence, if the initial assumption is correct, the average female must spawn about four times during the breeding season.

Frequency of Spawning in Nature

To test the prediction of spawning frequency derived above, spawning periodicity was determined from direct, visual observation of breeding events in the field. In 1978, I discovered a large spawning site in Salem Harbor, MA, where numerous eggs of *M. menidia* were deposited amongst mats of filamentous algae in the upper intertidal zone. Salem Harbor is located 20 km southwest of Essex Bay; however, individuals in each area are likely members of the same population because extensive mixing occurs during the offshore winter migration (Conover and Murawski 1982). Electrophoretic studies of geographic variation in *M. menidia* also support this contention (Johnson 1975).

Daily observations of the number of spawning aggregations sighted during high tide at Salem Harbor in 1979 showed that populations of Atlantic silversides breed on a semilunar periodicity coinciding with new and full moons (see figure 2 in Conover and Kynard 1984). Middaugh (1981) has reported similar observations based on a 3-yr study of populations in South Carolina. Within each semilunar spawning period of 1979 in Salem Harbor, the majority of spawning (40-90%) occurred on a single day, suggesting that females spawn, at most, once per semilunar cycle. This conclusion is further supported by the observation that sex ratios in spawning aggregations were highly male biased, whereas during nonspawning intervals, the sex ratio was near unity (Conover 1984). The sex ratio data is explained if females spawn, at most, once per cycle, while males spawn each day of a spawning period.

During 1979 in Salem Harbor, there were five semilunar spawning periods, although the first in late April was very light. In Essex Bay during 1977, there were four semilunar phases during the period defined as the breeding season. Hence, estimated spawning frequency based on gonadal analysis and direct observations of spawning fish agreed closely.

Spawning Frequency and Egg Production in the Laboratory

Females held in laboratory tanks, whether housed individually indoors or outdoors in groups where natural day and night illumination was present, did not maintain a fortnightly spawning periodicity. Instead, spawning occurred much more frequently: the interval between spawnings averaged about 4 d/female (Table 1; see also figure 4 in Conover and Kynard 1984). Batch fecundity averaged 99-187 eggs/g ovary-free body weight among different tanks. Total egg production averaged 1,425-3,375 eggs/g ovary-free body weight. Hence, the experi-

TABLE 1.—Egg production by *Menidia menidia* on unlimited food rations in the laboratory. Field data are also provided for comparison.

	No. of females	Mean ♀ body weight (g)	Days from 1st to last spawning	No. of egg batches per ♀	Days between spawn per ♀	No. eggs/g ♀ body weight per egg batch	Total eggs per ♀ (no.)	Total eggs/g ♀ body weight (no.)
Pool 1	4	6.32	63	15.25	3.9	99.0	9,551	1,511
Pool 2	4	5.82	51	11.75	3.7	121.2	8,299	1,426
♀ A	1	3.9	72	20.0	3.6	169.5	13,218	3,389
♀ C	1	3.6	[1]28	[1]7.0	4.0	187.0	[1]4,710	[1]1,308
Field	—	—	60-75	4.0	14-15	180-266	5,000	893 ± 197

[1]Low values reflect the fact that ♀ C died before the conclusion of the experiment.

mental fish responded to laboratory conditions by reducing batch fecundity somewhat, but spawning more frequently, and thereby producing about twice the number of eggs as in nature (Table 1). The daily rate of egg production was 24-47 eggs/g female body weight per d in the laboratory, but averaged about 14 eggs/g female body weight per d in the field.

At the termination of the experiment, four of the eight females in the outdoor pools were spent, three contained only recruitment eggs, and one had both recruitment and maturing eggs. Female A died of unknown causes after its last spawning on 22 July. Female C also died (9 June) before cessation of spawning by jumping out of the tank.

The total weight specific egg production for the experimental fish was generally within the range of total eggs available prior to the beginning of the breeding season. The one exception was female A which produced about twice the total number of eggs that a fish of its size should have had available at the beginning of the spawning season (see Figure 3). Hence, under certain laboratory conditions, females may be capable of producing new oocytes from oogonia during the breeding season, as recruitment eggs become depleted. These laboratory observations show that the reproductive patterns of egg maturation and spawning which are highly synchronized with and influenced by environmental factors in the field, easily become disrupted when individuals are removed from their natural habitat.

CONCLUSIONS

This study indicates that annual fecundity in *Menidia menidia*, and perhaps certain other fishes, can be estimated from the difference between total number of eggs (recruitment plus maturing) prior to the breeding season and recruitment egg retention near the end of the breeding season. Dividing the estimated total number of eggs shed per female by mean batch fecundity provided an estimate of spawning frequency. The accuracy of this value for spawning frequency was tested and found to agree closely with the spawning frequency inferred from direct field observations of breeding fish. Previous estimates of the fecundity of *M. menidia* were about 3-10 times less than that reported here because spawning frequency was not determined (Bayliff 1950; Jessop 1983). The studies of Hunter and his coworkers on northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980; Hunter and Macewicz 1980; Hunter and Leong 1981), and DeMartini and Fountain (1981) on queenfish, *Seriphus politus*, have amply demonstrated that estimates of annual fecundity can be in error by over an order of magnitude when multiple spawning is ignored.

The estimation of fecundity from the difference between total prespawning fecundity and recruitment egg retention is dependent on the assumption that new oocytes are not simultaneously produced from oogonia and added to the reservoir of recruitment eggs as mature eggs are spawned. Agreement between predicted and observed spawning frequency suggests that this may be true in *M. menidia*. Many more recruitment eggs were present in ovaries at the beginning of the spawning season than were actually spawned in nature. Evidently, the recruitment egg pool is largely formed before the breeding season in *Menidia*, as is believed for some other seasonal spawners (Tokarz 1978; Jones 1978; Baggerman 1980). However, the generality of this pattern in other multiple spawning temperate or tropical fishes is not clear. Clark (1925) noted that the relative abundance of mature, intermediate, and immature eggs in *Leuresthes tenuis* was relatively constant during the breeding season and concluded from this that new oocytes must be continuously produced to replenish those spawned. Taylor and DiMichele (1980) reached a similar conclusion based on the relative abundance of different developmental stages of oocytes during the semilunar spawning cycle of *Fundulus heteroclitus*. However, analyses based on relative proportions do not take into account that gonad weight (GSI) generally declines as the season progresses (e.g., Fig. 2) and that number of eggs in the most advanced mode is not necessarily constant during the breeding season. Comparison of the relative abundance of egg sizes from sections of an ovary may not reflect changes in absolute number. For example, the relative abundance of recruitment eggs in *M. menidia* during 1977 was 0.88 on 6 May, 0.78 on 6 June, 0.76 on 22 June, and 0.79 during 6-13 July. Hence, the relative proportion of recruitment eggs did not consistently decline during the breeding season even though the absolute number of eggs declined by a factor of 2.4. In any event, too little is known about patterns of oocyte growth in fishes to recommend that the annual fecundity of multiple spawners can generally be determined by monitoring the decline in the standing stock of ova as was done here. For instance, in tropical species that breed most of the year recruitment eggs may be produced continuously. Whenever possible, the results of several different approaches to estimating fecundity should be compared.

The results of the laboratory study demonstrated that *M. menidia* is physiologically capable of spawning much more frequently and over a shorter interval

than normally occurs in the field. The reasons for the higher spawning frequency and cumulative egg production for fish in captivity are probably several. Fecundity may have been increased because ration size was unlimited. Fecundity is dependent on the food supply in many species (Wootton 1979). In the stickleback, *Gasterosteus aculeatus*, (Wootton 1977) and the convict cichlid, *Cichlasoma nigrofasciatum*, (Townsend and Wootton 1984) experimental studies have demonstrated that the number of spawnings was positively related to food ration and the interval between spawnings was inversely related to ration.

In my experiments on *M. menidia*, spawning frequency may also have been increased beyond that in nature due to the continuous availability of appropriate spawning substrates and lack of tidal spawning cues in the laboratory. Conover and Kynard (1984) noted that both marine and freshwater populations of *Menidia* spp. tend to spawn during midmorning, and speculated that spawning in nature may be restricted by the fact that suitable spawning substrates are covered by high tide during midmorning only at fortnightly intervals. Correspondingly, a lacustrine population of *M. beryllina* spawns daily at midmorning (Hubbs 1976). Hence, in the laboratory where tidal cues are removed, spawning substrates are continuously available, and food is abundant, *M. menidia* responded by spawning more frequently. The high egg production of female A also suggests that if the supply of recruitment eggs is exhausted, new recruitment eggs can be formed. It is clear that estimates of fecundity in natural populations of multiple spawners based on laboratory studies alone should be interpreted with caution.

Many aspects of the fecundity and spawning periodicity of *M. menidia* are paralleled in a west coast atherinid, *Leuresthes tenuis*. The California grunion has a well-known semilunar spawning cycle (Walker 1952). Clark (1925) conducted a detailed study of egg diameter frequencies in ovaries of *L. tenuis* and concluded that each female spawns once about every 15 d. Batch fecundity was very similar to that reported here for *M. menidia*. Although Clark measured batch fecundity in only a few individuals, a 118 mm grunion contained 1,613 ova. I calculate that a 118 mm Atlantic silverside would be expected to have 1,704 ripening eggs during the middle of the breeding season. Clark also found retention of recruitment eggs at the end of the breeding season and presented histological evidence that retained eggs were being resorbed.

Based on my estimate of the average annual fecundity of *M. menidia* (893 ± 197 eggs/g ovary-free body weight) and the wet weight of ripe eggs (0.8 g/1,000 eggs), an Atlantic silverside produces nearly 0.7 of its body weight in eggs during the breeding season in nature. In the laboratory, females produced 1.1-2.7 times their body weight in eggs. Studies of other multiple spawners have yielded similar results. DeMartini and Fountain (1981) estimated that the queenfish could spawn about 114% of its body weight in a year. Experiments on several species of cyprinids indicate that they are capable of spawning 0.7 to 6.8 times the volume of the female in eggs, at least in the laboratory (Gale and Gale 1977; Gale and Buynak 1978, 1982; Gale 1983). Hubbs (1976) estimated that a freshwater population of *Menidia beryllina* spawned 6-8 times female weight in eggs, although his assumption that each female spawns daily throughout the length of the breeding season needs further documentation.

Subseasonal trends in batch fecundity among multiple spawners have been examined by few investigators. If trends in batch fecundity within the breeding season are the adaptive result of natural selection, then periods of maximum batch fecundity should reflect the period when the probability of offspring survival is greatest. On the other hand, trends in batch fecundity could simply result from varying food conditions for adults. Three general relationships between the batch fecundity and the time of the breeding season have emerged from field studies with which I am familiar. These include 1) constant batch fecundity during the breeding season (Fig. 6, curve A), 2) a concave downward relation between batch fecundity and the breeding season (Fig. 6, curve B), and 3) a constant decline in batch fecundity during the breeding season (Fig. 6, curve C). Constant fecundity (curve A) might be expected where the optimal environmental conditions for reproduction and offspring survival are constant or vary unpredictably during the breeding season. This pattern has been found in the queenfish (DeMartini and Fountain 1981), a pelagic spawner of the western North American coast where aperiodic upwelling events produce unpredictable variations in plankton productivity and potential larval survival (Lasker 1978). When seasonal environmental conditions change in a predictable manner, there may be an optimal period for reproduction that occurs at roughly the same time each year, and batch fecundity would be expected to be maximal at that time (curve B). In *M. menidia*, the relation between batch fecundity and the breeding season was concave downward, suggesting that reproductive success is maximal during the middle of the breeding season. There is some independent evidence to support this hypothesis. Winter mortality during the offshore migration is

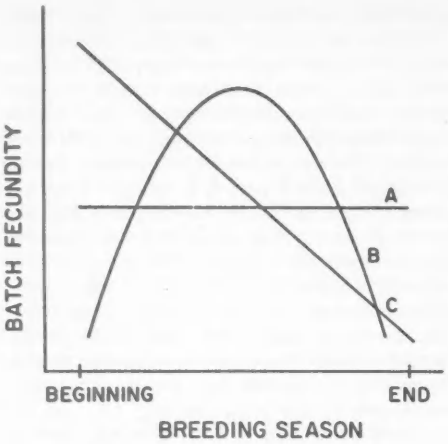

FIGURE 6.—Three hypothetical relationships between batch fecundity and time of the breeding season that have empirical support in the literature. A) Constant batch fecundity. B) Batch fecundity maximal during the middle of the breeding season. C) Batch fecundity maximal at the beginning of the breeding season and declining continuously thereafter.

strongly size-selective in *M. menidia* (Conover and Ross 1982; Conover 1984): the largest young-of-the-year have the highest probability of surviving. Hence, there should be selection pressure to breed as early in the spring as physical conditions (such as temperature) permit, and perhaps before conditions are optimal. Any offspring that managed to survive early in the breeding season will ultimately benefit from having a longer growing season. Conversely, towards the end of the breeding season, energy placed into reproduction becomes wasted because these offspring will have almost no chance of growing to a size that will permit winter survival. It follows that somewhere in the middle of the breeding season will be the optimal period for reproduction. Declining batch fecundity during the breeding season (curve C) has been reported for a population of the common mummichog, *Fundulus heteroclitus*, where batch fecundity was greatest at the beginning of the breeding season and became progressively less thereafter (Kneib and Stiven 1978). A continuous decline in batch fecundity may evolve when the value of putting energy into current reproduction, as opposed to somatic growth, declines continuously as the breeding season progresses. Although few data are now available for comparing the subseasonal patterns of batch fecundity in multiple spawning fishes, such information may eventually prove useful in understanding the general reproductive strategies of fishes.

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PARASITES OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*: FISHERY IMPLICATIONS

R. J. G. LESTER,[1] A. BARNES,[2] AND G. HABIB[3]

ABSTRACT

The numbers of 26 types of parasites were counted in 878 fish, of which all but 3 were from 14 areas in the Pacific. Data from the 22 most reliable parasites gave no evidence of discrete stocks of skipjack tuna in the Pacific, either when analyzed singly or when using combinations of parasites in multivariate analyses. New Zealand fish carried many tropical parasites, particularly didymozoids, in numbers similar to fish caught in the tropics, indicating that the bulk of these fish had recently migrated from the tropics. The number of *Tentacularia coryphaenae*, a larval tapeworm, was positively correlated to fish size in the tropics. In New Zealand, however, fish over 55 cm carried about the same number of *T. coryphaenae* as fish 45 to 55 cm, suggesting they had left the tropics when they were 45 to 55 cm and had not returned.

Analysis of the numbers of parasites from particular schools suggested that school members stayed together for several weeks but not for life.

The use of parasites to delineate stocks for management purposes is a well-established technique. For a comprehensive review of the many examples see MacKenzie (1983).

The skipjack tuna, *Katsuwonus pelamis*, is one of the most valuable fishery resources of the central and western Pacific. At least 50 species of parasites have been reported from it. The distribution of only one, the hemiuroid digenean *Hirudinella ventricosa*, has previously been investigated. In the Atlantic, Watertor (1973) found it in 7% of skipjack tuna off West Africa, 40% off Brazil, and < 1% off Florida. In the Pacific, Nakamura and Yuen (1961) found it in 21% of skipjack tuna off the Marquesas and 34% of fish from Hawaii. Sindermann (1961) pointed out that analyzing the distributions of combinations of parasites may provide more information than the examination of individual species. That, in general, has been our approach here.

In addition, school-school variation in parasite numbers was studied to determine how long schools stayed together, and secondarily to evaluate the degree of permanence of the parasites.

MATERIALS AND METHODS

Of the 878 fish dissected, 386 were collected by the *Hatsutori Maru* on charter to the South Pacific Commission (SPC), 246 by the New Zealand Ministry of Agriculture and Fisheries (NZ), and the remainder by other governments and fishing companies (see Acknowledgments). Fish were obtained from 15 areas (Fig. 1, Table 1).

Gills and viscera were frozen and flown to Brisbane for dissection. The SPC and NZ fisheries officers sampled 5 fish/school from a maximum of 3 schools/d. Commercial companies were unable to sample from individual schools and usually supplied the head and the anterior ventral body, removed from frozen fish by a single slanting cut using a band saw. Fork length, if not supplied, was calculated

TABLE 1.—Sources of fish dissected.

	Area	Date	No. fish	Avg. length (cm)
A	Palau, Helen R.	Aug. 1980	35	41
B	Ponape	July 1980	45	59
C	Papua New Guinea	June 1981	30	50
D	Papua New Guinea	Nov. 1981	60	41
E	Solomon Is.	June 1980	30	46
F	Coral Sea	Jan. 1982	19	57
G	Fiji	Feb., Mar., Apr., May 1980	100	50
H	Norfolk Is.	Mar. 1980	21	57
I	New South Wales	Jan. 1981	103	47
J	New Zealand, west	Mar. 1980; Jan., Feb. 1982	69	52
K	New Zealand, east	Jan. 1980; Jan., Feb. 1982	163	49
L	Marquesas	Dec. 1979; Jan. 1980	150	47
M	California	Aug. 1981	30	47
N	Ecuador	Jan. 1982	20	48
O	Atlantic (Puerto Rico)	Mar. 1981	3	50

[1]Department of Parasitology, University of Queensland, St. Lucia, Brisbane, Australia 4067.
[2]Faculty of Science, University of Queensland, St. Lucia, Brisbane, Australia 4067.
[3]Fisheries Research Division, New Zealand; present address: Southpac Fisheries Consultants, P.O. Box 7230, Auckland 1, New Zealand.

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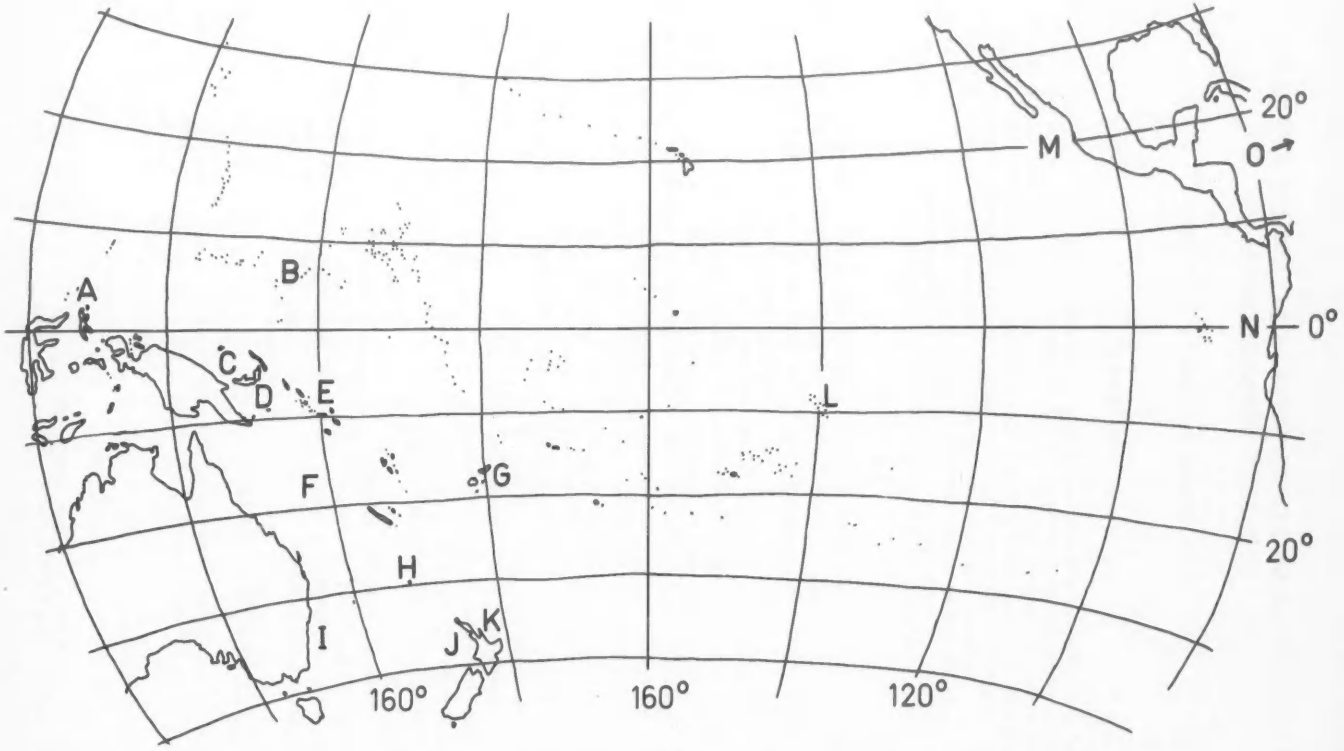

FIGURE 1. – The 15 sites, A to O, from which fish were received for parasitological analysis. A = Palau, Helen Reef; B = Panape; C and D = Papua New Guinea; E = Solomon Islands; F = Coral Sea; G = Fiji; H = Norfolk Island; I = New South Wales; J = New Zealand West; K = New Zealand East; L = Marquesas Islands; M = California; N = Ecuador; O = Atlantic (Puerto Rico).

from head length using the formula 7.8 + 2.75 × (head length) for heads under 14.5 cm and −1.7 + 3.3 × (head length) for larger heads (from measurements of 80 and 83 fish, respectively). Prior to dissection, fish were thawed overnight at 6°C. In general, all viscera parasites were counted whereas gill parasites were counted on one side only and the numbers doubled in the final tables. A didymozoid capsule was counted as one parasite though most contained two individuals. Representative parasites were fixed and stored in 10% Formalin[4] except for nematodes which were fixed and stored in 70% alcohol.

An additional set of data on the abundance of the larval cestode *Tentacularia coryphaenae* was collected at sea by SPC and NZ fisheries officers. They recorded the number of *Tentacularia* visible through the peritoneum in the wall of the body cavity of 1,529 fish.

Besides some summary statistics, two types of statistical analysis were done: 1) investigation into the similarities and dissimilarities of the parasite fauna between the various areas sampled, and 2) a study of school integrity.

The similarities and dissimilarities between areas were examined using a series of cluster analyses and multivariate canonical analyses (Mardia et al. 1979). Strictly speaking, canonical analyses require data which are normally distributed and which have a common variance. However, the frequency distributions of the parasites were not normal. They showed considerable differences from one parasite to another and most appeared to have two components: one which could be adequately approximated by a negative binomial distribution; and a second component consisting of a disproportionately large zero category, presumably arising because some schools had not been exposed to infection. Precise transformations to normalize the data would thus have been complex and of doubtful accuracy considering the small size of the samples from each school. A single transformation for all species was therefore used: the natural logarithm of the number of parasites plus 1.0.

To avoid possible biases due to associations between parasite numbers and fish length, such as that shown in Figure 2, the transformed counts were then adjusted for fish length. This was done for each species by regressing log (parasite number + 1.0) on fish length, for all Pacific tropical fish (489), to estimate the magnitude of any relationship. This was used to adjust the transformed parasite numbers, except where this was zero, to that expected for a fish of a standard length of 50 cm. (This length was very close to the overall mean length of the fish.) The method could not be trusted to eliminate all effects of length, so, as an added safeguard, only fish 39.5 to 57.5 cm were used in the multivariate analyses (83% of the total). These are likely to have been 1 yr old (Uchiyama and Struhsaker 1981; Wankowski 1981).

In a few instances a parasite was absent from all fish in one area. To allow matrix inversion in the canonical variate analyses, a random number between −0.005 and +0.005 was added to the data. This did not influence the outcome. The results of the canonical variate analyses were displayed graphically as plots of the first versus the second canonical

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

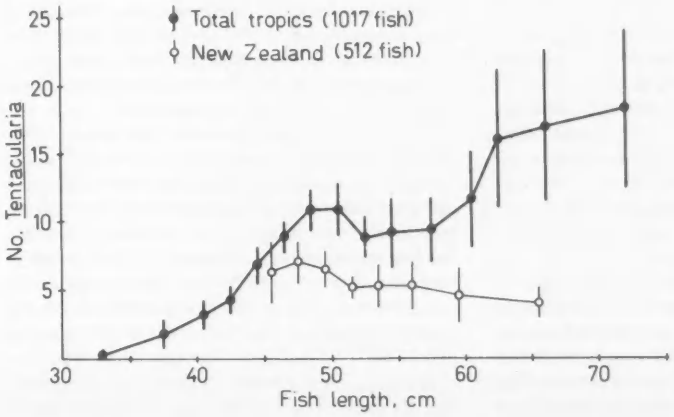

FIGURE 2.—Relationship between number of *T. coryphaenae* and fish length. Mean ±2 SE. Each mean from minimum of 19 fish. In the tropics the number increased with length but this was not reflected in the New Zealand samples.

axes. Confidence limits (95%) for the positions of different areas on these plots are presented as circles with radius equal to the square root of 5.99/number of fish in sample (Mardia et al. 1979).

Analyses on the same combinations of parasites were also done by calculating minimum spanning trees (Gower and Digby 1981), and dendrograms from nearest neighbor and centroid cluster analyses (Clifford and Stephenson 1975), basing similarity measures on logarithms of area means. Areas were grouped in a similar way by all methods. Using clustering algorithms which either ignored or allowed for matches between areas where parasites were not recorded did not significantly influence results. For these reasons, and because only canonical variate analysis provided some measure of reliability for its conclusions (confidence rings), only the results of the canonical analyses are presented below.

School integrity was examined by comparing the variability in parasite numbers per fish between schools, to that within schools, for the two areas (Marquesas and east New Zealand) where the largest numbers of schools were sampled. This showed which parasites were strongly linked to schools, and also allowed tentative estimation of the length of time schools remained intact. In theory, for parasites to show strong school associations two conditions need to be met: the parasite must heavily infect some schools and not others, and its life span in the fish must be equal to or shorter than the life of the school. Parasites which showed strong school-school association were therefore likely to be shorter lived than those not showing such associations, and other evidence being equal, were considered less reliable as population markers than related species.

Two methods were used to compare within and between school variability in each of the two areas. First, a series of univariate analyses of variance of log (parasite numbers + 1.0) were done to calculate the ratio of between school to within school variances. The magnitude of these ratios, and the corresponding probabilities that they do not differ from 1.0, were interpreted as measures of school integrity. A limitation of this method was that the data were only approximately normally distributed, particularly for rare parasites, and thus the derived probabilities were also approximations.

The second method, a median test, was based on the binomial distribution. The number of parasites of a particular species in each fish was transformed to a zero if it was less than or equal to the median number per fish for the area, and to a one otherwise. The zeros and ones of each school were then considered as a binomial sample. If these samples showed evidence of greater variation than expected by chance (i.e., too many schools with nearly all zeros or nearly all ones), then the schools differed with respect to the distribution of the parasite. A statistic, approximately distributed as a χ^2 random variable, was calculated using GLIM (Baker and Nelder 1978) to determine whether the binomial samples showed evidence of differences. Its associated probability was used as a measure of school integrity. The method had the useful property of being independent of the distribution of parasite numbers. For parasites with a median per fish of <1, the test was based on the presence or absence of the parasite, though obviously the rarer the parasite the less sensitive the test.

It is possible that some schools were sampled twice. If this did happen, the results of both methods err on the conservative side. Only those species that gave consistent results by both methods were used to draw conclusions about school integrity.

RESULTS

Evaluation of Parasite Species

Information was collected on 26 different types of parasites (species or species complexes) from 15 areas. A summary of the raw data unadjusted for fish length is given in Table 2.

The parasite species were evaluated for their probable longevity on or in skipjack tuna. For them to be useful as markers they needed to be relatively long-lived, preferably surviving for the life of the fish. Nothing was known specifically about their longevity in skipjack tuna, though data were available on related forms (Table 3). In general, intestinal lumen dwellers appear to be more easily lost than larval forms encapsulated in the tissues. The 26 skipjack tuna parasites were divided into four groups, those considered "temporary", "semi-permanent", and "permanent", and those not used at all.

Four parasites were not used in any analyses. Two of the nematodes, *Ctenascarophis* sp. and *Spinitectus* sp. (Nos. 23 and 24 in Table 2), were found in the gut of virtually every fish in which they were sought, from every area. Their small size meant that the number recovered was a function of the time spent searching. They were only counted in every fifth fish, as were the two larval cestodes from the large intestine, *Scolex polymorphus* (large) and *S. polymorphus* (small) (Nos. 25 and 26). Counting these was time consuming, their apparent abundance may have been inversely related to the state of preservation of

TABLE 2.—Average numbers of parasites per fish in all skipjack tuna (878) from the areas listed in Table 1, unadjusted for length. The last column gives the correlation coefficient (r) for length against log (parasite number + 1) for Pacific tropical fish.

No.	Parasites	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	r
1	*Caligus* spp.	5	17	5	5	10	36	4	3	3	3	1	7	0	1	7	0.37
2	*Didymocylindrus filiformis*	16	5	2	3	4	4	7	3	6	8	10	4	4	3	10	−0.14
3	*Didymocylindrus simplex*	16	7	4	6	13	11	14	12	18	26	18	14	15	6	3	−0.08
4	*Didymoproblema fusiforme*	4	1	0	1	1	1	4	1	4	2	3	3	3	1	1	−0.06
5	*Lobatozoum multisacculatum*	0.1	0.1	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.1	0.4	0.2	0.3	0.1	0.0	0.03
6	*Syncoelium filiferum*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	13.1	0.0	0.0	0.0	0.0	0.0	0.0	—
7	*Philometra* sp.	1	3	4	29	5	P[1]	2	2	3	3	1	6	6	1	8	0.02
8	*Anisakis* type I	1.0	0.2	2.7	1.0	0.7	1.6	0.2	0.5	0.9	2.1	1.5	0.6	0.2	0.1	2.7	0.13
9	*Anisakis* type II	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.4	0.1	0.8	0.2	0.0	0.4	1.2	2.3	−0.02
10	*Terranova* sp.	0.0	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.06
11	*Coeliodidymocystis* sp.	1.3	2.1	0.3	0.2	0.9	0.2	1.2	0.5	0.3	0.7	1.3	0.8	0.1	0.7	0.0	0.03
12	*Tentacularia coryphaenae*	3	22	P[1]	3	4	19	8	6	4	5	6	10	3	P[1]	P[1]	0.48
13	*Oesophagocystis dissimilis*	12	6	8	7	8	12	9	3	6	3	9	8	8	9	11	−0.05
14	*Kollikeria* / *Didymocystis* spp.	13	4	1	5	9	4	7	7	8	4	5	6	11	5	6	−0.11
15	*Dinurus euthynni*	55	9	19	35	66	1	2	3	0	0	0	15	0	0	0	−0.34
16	*Didymocystoides intestino-muscularis*[2]	30	27	26	37	49	39	54	18	15	12	16	44	134	17	54	−0.14
17	*Hirudinella ventricosa*	0.4	0.6	0.4	0.2	1.1	0.7	0.4	0.3	0.1	0.0	0.0	1.1	0.1	0.2	1.0	−0.10
18	*Raorhynchus terebra*	22	16	13	17	15	18	25	65	4	2	4	12	3	1	0	−0.00
19	*Didymocystoides intestino-muscularis*[2]	14	3	3	9	3	8	5	8	6	6	6	7	13	3	2	−0.24
20	*Lagenocystis* / *Univitellannulocystis* spp.	76	40	29	29	22	45	43	16	38	17	30	61	178	34	41	−0.11
21	*Tergestia laticollis*	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.8	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.00
22	*Rhipidocotyle* sp.	0.0	0.3	0.0	0.2	0.2	2.3	2.4	0.0	1.3	0.0	0.0	0.1	0.0	0.0	0.0	0.08
23	*Ctenascarophis* type	35	7	6	2	18	22	38	49	7	17	21	33	4	1	108	
24	*Spinitectus* type	10	7	20	2	12	5	9	10	5	6	18	13	5	3	10	
25	*Scolex polymorphus* (large)	4	0.4	0.2	0	7	166	33	P[1]	122	101	27	10	161	9	7	
26	*Scolex polymorphus* (small)	200	124	1,089	287	8,900	257	463	140	211	53	24	206	495	153	105	

[1]P = present.
[2]No. 16—stomach; No. 19—intestine.

the fish, and their longevity was doubtful. *Philometra* sp. (No. 7) was found predominantly in developed ovaries, which were present in less than half of the fish sampled. The data were used for comparing school-school variability only.

Seven parasites were considered "temporary". They appeared to be short-lived or easily lost from the fish. The caligoid copepods (No. 1, primarily *Caligus productus* in the tropics and *C. bonito* in temperate waters) were not permanently attached and probably moved from fish to fish (Kabata 1981). *Syncoelium filiferum* (No. 6) was common on the gills in New South Wales and New Zealand samples (I, J, and K), but was not recovered from anywhere in the tropics. It is common on fish endemic to New Zealand (D. Blair[5]). It was considered possibly a temperate short-lived parasite, at least on skipjack tuna, and this was verified by the school integrity study and by conventional tagging data (see later).

Some hemiurids are known to be readily lost from the gut of other species of fish (Table 3). Margolis and Boyce (1969) observed that over half the *Lecithaster gibbosus* were lost from salmon fingerlings within 3 wk of bringing the fish into captivity. We found *Dinurus euthynni* (No. 15) in all tropical samples from the central and western Pacific but not in the temperate samples I, J, and K. As it showed strong school associations and as the didymozoid data described later showed that New Zealand fish had a recent origin in the tropics, *D. euthynni* was evidently a short-lived tropical parasite that was lost as the fish migrated south. This also appeared to be true for *Hirudinella ventricosa* (No. 17) and possibly for two relatively rare gut-lumen digeneans, *Tergestia laticollis* (No. 21) and *Rhipidocotyle* sp. (No. 22).

In other fish, adult acanthocephalans may be short lived (Table 3). Möller (1976) found that over half the *Echinorhynchus gadi* in three species of fish were lost within 2 wk of the fish being brought into captivity. In our data, *Raorhynchus terebra* (No. 18) was present in reduced numbers in I, J, and K, suggesting it was lost in southern waters. All these parasites then were labelled "temporary".

Didymozoid digeneans were considered "semi-permanent" parasites. In other fish, some didymozoids, or at least the remains of them, are believed to stay in the tissues for the life of the fish. Others, including some species found in the gonads or gills, are lost annually (Table 3). In general, therefore, skip-

[5]D. Blair, Department of Zoology, University of Canterbury, Christchurch, New Zealand, pers. commun. September 1984.

TABLE 3.—Probable maximum life spans of parasites related to those found in skipjack tuna.

Parasite	Site	Host	Life span	Reference
Acanthocephala				
Echinorhynchus gadi	Intestine	*Zoarces viviparous*	2 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Gadus morhua*	6 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Myxocephalus scorpius*	7 wk	Moller (1976)
Echinorhynchus gadi	Intestine	*Platichthys flesus*	11 wk	Moller (1976)
Acanthocephalan sp.	Intestine	*Sparus aurata*	< 8 wk	Paperna et al. (1977)
Hemiurid Digenea				
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	< 9 mo	Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*Oncorhynchus gorbuscha*	> 5 mo	Margolis and Boyce (1969)
Lecithaster gibbosus	Int. and caec.	*O. keta*	8 mo	Margolis and Boyce (1969)
Tubulovesicula lindbergi	Stomach	*O. keta*	> 31 mo	Margolis and Boyce (1969)
Lecithophyllum botryophorum	Stomach	*Argentina silus*	10 mo	Scott (1969)
Didymozoid Digenea				
Nematobothrium texomense	Ovary	*Ictiobus bubalus*	> 8 mo	Self et al. (1963)
Neometadidymozoon helicis	Buc. cav.	*Platycephalus fuscus*	1 yr	Lester (1980)
Nematobothrium spinneri (eggs)	Muscle	*Acanthocybium solandri*	> host	Lester (1980)
Larval Cestoda				
Gilquinia erinaceus	Mesentery	*Melanogrammus aeglefinus*	> host	Lubieniecki (1976)
Trypanorhynch sp.	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Triaenophorus crassus	Mesentery	*Oncorhynchus* spp.	> host	Margolis (1965)
Larval Anisakinae				
Larval anisakid	Mesentery	*Clupea harengus*	> 1 yr	Sindermann (1961)
Larval anisakid	Mesentery	marine fish	several years	Margolis (1970)
Porrocaecum decipiens	Mesentery	*Gadus morhua*	several years	Platt (1976)

jack tuna didymozoids were thought to be in the fish probably for at least several months. However, there was some suggestion that 3 of the 10 skipjack tuna didymozoids had a shorter adult life span than the others. Didymozoid No. 16 was much less common in New Zealand waters than in the tropics (Table 4), and didymozoid Nos. 19 and 20 were also less common and, in addition, showed strong school associations (see later). These three didymozoids (possibly representing four species) were omitted from the analysis for Figure 3.

The remaining four parasites (Nos. 8, 9, 10, and 12) were classed as "permanent". Larval cestodes and nematodes, particularly those found in the tissues, are generally believed to survive for several years, often for the life of the fish (Table 3). They have been used successfully many times as fish population markers (see MacKenzie 1983). In skipjack tuna, the larva of a trypanorhynch cestode, *Tentacularia coryphaenae*, was found in the wall of the body cavity and occasionally in the viscera. No degenerating forms were seen, suggesting that it survived for an extended period and hence could be an excellent population marker, though counts were not available from areas C, N, and O. Larval anisakids were found on the wall of the stomach or in the mesentery. The literature suggested that they should also be good long-term markers (Table 3). They were counted in all areas.

Protozoan parasites have been used successfully to separate stocks of several species of fish. However, none has been reported from skipjack tuna, and we found none in this study.

TABLE 4.—Average number of didymozoids in New Zealand fish (all lengths) compared with fish caught in the tropical western Pacific (areas A, B, C, D, E, F, G, and L). In parentheses, log $(x + 1)$ length-adjusted means for fish 40 to 57 cm only.

No.[1]	Parasite	New Zealand		Tropics	
2	*D. filiformis*	9	(1.1)	6	(0.8)
3	*D. simplex*	20	(1.7)	12	(1.3)
4	*D. fusiforme*	2.7	(0.6)	2.5	(0.5)
5	*L. multisacculatum*	0.3	(0.1)	0.1	(0.0)
11	*Coeliodidymocystis* sp.	1.1	(0.4)	0.9	(0.3)
13	*O. dissimilis*	7	(1.3)	9	(1.9)
14	*Kollikeria* / *Didymocystis* spp.	5	(1.2)	6	(1.5)
16	*D. intestinomuscularis*[2]	15	(1.8)	41	(3.3)
19	*D. intestinomuscularis*[3]	6	(1.3)	7	(1.4)
20	*L. katsuwoni* / *U. katsuwoni*	26	(1.9)	47	(2.3)
	No. of fish	232	(213)	469	(364)

[1]Code no. from Table 2.
[2]Stomach.
[3]Intestine.

Relationships Between Areas

Analyses of individual distributions of permanent and semipermanent parasites showed that the abundances of individual parasites varied across the Pacific. However, these differences were inconsistent, the pattern established by one parasite being in conflict with that of a second, and so on.

The data from the three anisakid nematodes and the seven didymozoids considered longest lived were therefore analyzed using canonical variate analysis. Because of the more permanent nature of these parasites and the completeness with which they were recorded from all areas, these data were considered the most reliable for statistically assessing the similarities and dissimilarities between areas. The first three canonical axes accounted for 75% of the

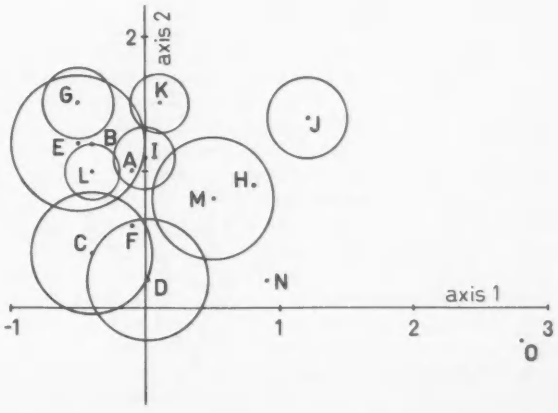

FIGURE 3.—Results of multivariate analysis using 3 "permanent" and 7 "semipermanent" parasites (Nos. 2, 3, 5, 8, 9, 10, 11, 13, and 14). Values for first two canonical vectors plotted, and 95% confidence rings indicated for samples of more than 24 fish. The letters refer to the sampling sites indicated in Figure 1.

variation in area-to-area differences in parasite numbers. A plot of the first two, accounting for 58% of the variation, showed the Atlantic fish (O) to be distinct from all the Pacific ones, even though only three fish from the Atlantic were dissected (Fig. 3). However, fish from California (M) and Ecuador (N) fell close to the western Pacific samples. They were separated out on the third axis (not shown), but nevertheless it is evident that they had a somewhat similar parasite fauna. The fish from western New Zealand (J) appeared distinct, and so too, to a less extent, were the Papua New Guinea samples (C and D). There is no suggestion that fish from Ponape (A), Palau (B), Solomon Islands (E), Fiji (G), and the Marquesas (L) had distinct faunas of these long-lived parasites.

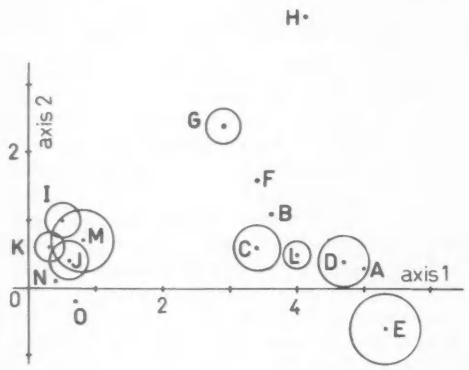

FIGURE 4.—Results of multivariate analyses using 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22). 95% confidence rings given for samples of more than 24 fish.

In this analysis, *Anisakis* II had the most powerful discriminating properties, though at least 7 of the 10 parasites used were capable of substantial discrimination in their own right.

An analysis based on the 7 "temporary" parasites (Nos. 1, 6, 15, 17, 18, 21, and 22) produced a much greater separation of areas (Fig. 4). They are grouped into two broad classes: one containing New South Wales (I), New Zealand (J, K), and the eastern Pacific (M, N); and the other the western tropical areas. Each area in the latter group had a temporary parasite fauna that was distinct from most other areas. Over 83% of the variation was accounted for by the first two axes, and 90% by the first three. It is interesting to note that New South Wales (I) is more similar to east New Zealand (K) than to west New Zealand (J) (this was much more marked on the third axis, not shown, where I and K were pulled to one side), and that west New Zealand is similar to California (M) and Ecuador (N).

Taken together, Figures 3 and 4 indicate that several distinct skipjack tuna parasite faunas existed within the tropical Pacific, and the longer lived parasites were more evenly distributed than the shorter lived ones.

To check these results and to look for links between the New Zealand fish and the tropical areas, the west Pacific data were reanalyzed using first the 10 "semipermanent" parasites (the didymozoids) and second the 4 "permanent" parasites (anisakids and *T. coryphaenae*).

The average numbers of didymozoids in the New Zealand fish were almost identical to the overall average for the central and western tropics (Table 4). In the multivariate analyses, the temperate water samples fell to one side of the tropical samples (Fig. 5

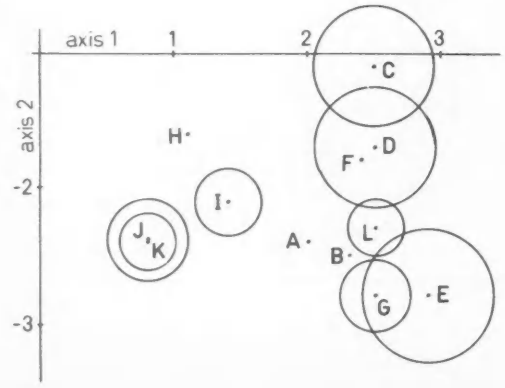

FIGURE 5.—Results of multivariate analysis using 10 didymozoids only (Nos. 2, 3, 4, 5, 11, 13, 14, 16, 19, and 20). 95% confidence rings given for samples of more than 24 fish.

–H, I, J, K), possibly because of the three didymozoids suspected of being relatively short-lived (Nos. 16, 19, and 20). The east and west New Zealand samples (J, K) were identical on the first two axes, and separated only slightly on the third axis (not shown). There was no obvious link between New Zealand and any particular tropical area.

Similarly, the larval nematodes and *T. coryphaenae* (Nos. 8, 9, 10, and 12) did not suggest a link between New Zealand fish and those from any particular tropical area (Fig. 6). However, west New Zealand (J) now appeared distinct from east New Zealand (K) and New South Wales (I). The separation was due to areas having either high *Anisakis* I and II and low *Terranova* and *T. coryphaenae* or low *Anisakis* I and II and high *Terranova* and *T. coryphaenae*. West New Zealand (J) was at one extreme (high *Anisakis*) and the three most northwestern areas–Ponape (B), Fiji (G), and Marquesas (L)–at the other. *Tentacularia coryphaenae* and probably *Terranova* were picked up in the tropics. It seems likely that one or both of the *Anisakis* larvae were picked up predominantly in temperate waters, particularly in west New Zealand. This may explain the separation of west New Zealand from the other areas in Figure 4.

In summary, the New Zealand fish were not closely aligned with any particular tropical sample, and the eastern and western New Zealand fish were probably carrying similar parasite faunas when they arrived in New Zealand.

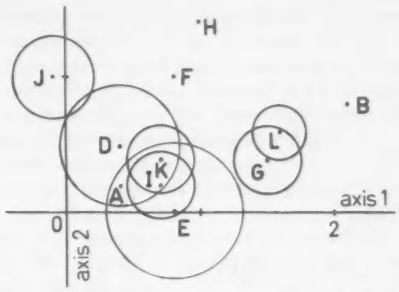

FIGURE 6.–Results of multivariate analysis using the four "permanent" parasites (anisakids and *T. coryphaenae*, Nos. 8, 9, 10, and 12). 95% confidence rings given for samples of more than 24 fish.

Tentacularia coryphaenae

Data on this parasite are presented in detail because we had more than for any other parasite and because potentially it was our most valuable marker. It also was the subject of many queries from skipjack tuna processors. The parasite was common throughout the south, central, and west Pacific (Table 3, parasite No. 12). The means of samples of over 22 fish within the length range 44 to 53.9 cm suggested an east-west cline across the Pacific, with twice as many parasites being found in fish from around the Marquesas (L) as around Papua New Guinea (C and D) (Fig. 7). A regression analysis of number of parasites against longitude using tropical data on the number of parasites in 972 fish, transformed and adjusted for differences in host length (data collected independently by the SPC), showed that the relationship was statistically significant, though it only accounted for about 7% of the fish-to-fish variation.

Considering fish of all sizes, the number of *T. coryphaenae* in the tropics increased with the size of the fish (Fig. 2, solid circles). The increase around 47 cm is due to many of the Marquesas fish being this size and Marquesas fish tended to have more *T. coryphaenae*. In New Zealand, smaller fish had about the same average number as fish from the tropics. However, this number did not increase with size (Fig. 2, open circles). Thus, the 58+ New Zealand fish had fewer parasites than their peers in the tropics, and about the same number as the 45 to 50 cm fish.

School-to-School Variation

An analysis of variance, and a median test, were carried out on 30 schools from the Marquesas and 19 schools from eastern New Zealand (areas L and K, respectively, Table 5). The results of the two methods on each data set show close agreement.

In the Marquesas, five parasites showed strong evidence of association with particular schools, i.e., the probability that schools differed was at least 0.95 with both methods. The parasites were *Caligus* spp. (No. 1), *D. euthynni* (No. 15), *H. ventricosa* (No. 17), *D. intestinomuscularis* (No. 19), and *Lagenocystis*/*Univitellannulocystis* spp. (No. 20). For these parasites to show significant differences, they must have heavily infected some schools and not others, and their life span in the fish must have been equal to or shorter than the life of the school. The literature review suggested that the first three species could possibly be readily lost from fish, and this is vindicated by their strong school association. The evident impermanence of the last two, however, was unexpected. It was as a consequence of this finding that they were not included in the analysis for Figure 3.

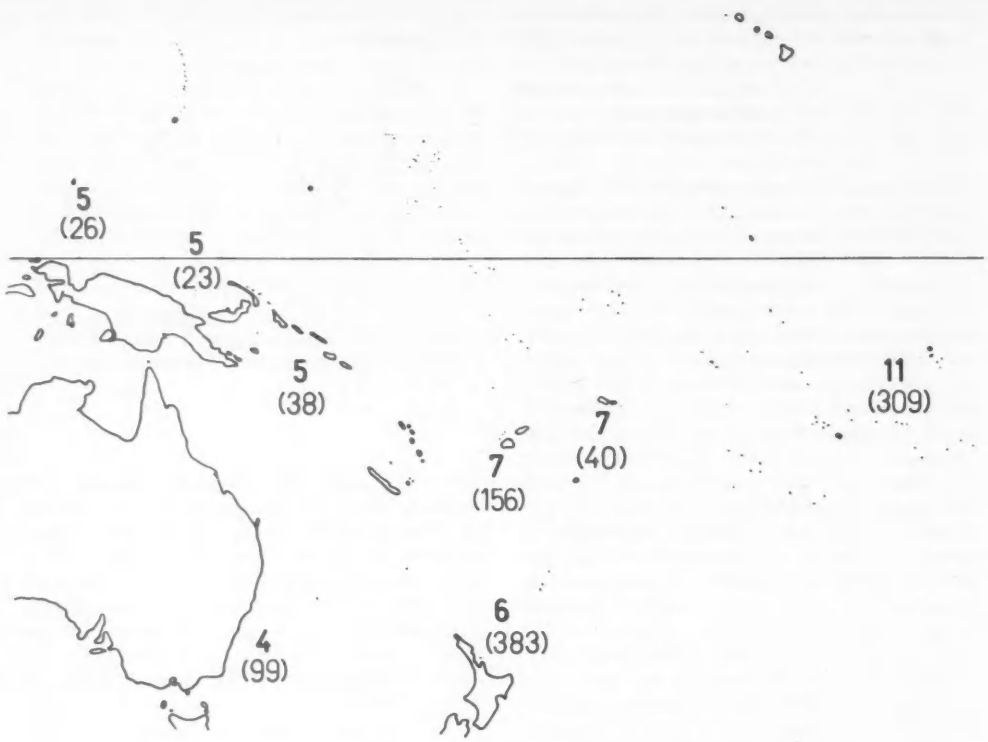

FIGURE 7.—The average numbers of *T. coryphaenae* in skipjack tuna 44 to 53.9 cm long in samples of over 22 fish. Note that the number increased to the east. (In parentheses, number of fish sampled.)

Several other parasites thought to be short-lived, such as *R. tereba*, did not show up in the test, presumably because their infective stages were relatively evenly distributed in the tropical Pacific.

In New Zealand, parasites showing close association with particular schools (using both tests) were *L. multisacculatum* (No. 5), *S. filiferum* (No. 6), *Philometra* sp. (No. 7), *Coeliodidymocystis* (No. 11), *T. coryphaenae* (No. 12), *R. terebra* (No. 18), and *D. intestinomuscularis* (No. 19). *Syncoelium filiferum* and *R. terebra* were both thought to be temporary parasites that could be gained in New Zealand or adjacent waters (Norfolk Island). The origin of the *Philometra* was unknown. Their number reflected the state of maturity of the fish and this varied between schools. However, we were left with three didymozoids and *T. coryphaenae*, all of which differed markedly between schools in eastern New Zealand. One of the didymozoids, *L. multisacculatum*, a normally rare tropical parasite, was found on all five fish from one school (numbers per fish 1, 2, 8, 3, and 1). As the three didymozoids and *T. coryphaenae* are essentially tropical parasites, the schools had evidently not fully mixed while in temperate waters.

If this is true, these four parasites could not have been picked up uniformly across the Pacific. Evidence is given above that *D. intestinomuscularis* (No. 19) was not picked up uniformly even within the Marquesas. For the other species, a comparison of their mean numbers per fish per school in different areas of the tropical Pacific showed that *Coeliodidymocystis* sp. and particularly *T. coryphaenae* were indeed more abundant in some areas than others. *Lobatozoum multisacculatum* was too rare for any conclusions to be drawn in this respect.

TABLE 5.—Comparison of within and between school variability in numbers of parasites per fish for two areas.

Parasite no. (see Table 3)	Marquesas		New Zealand	
	Analysis of variance[1]	Median test[2]	Analysis of variance	Median test
1	***[3]	***		
2		**		
3		*		
4				
5			***	**
6	(no parasites found)		***	***
7			*	*
8		*		
9				
10			(no parasites found)	
11			*	*
12			*	***
13				*
14				
15	***	**	(no parasites found)	
16				
17	*	*		
18			***	***
19	***	***	*	***
20	**	***		
21	*			
22				

[1]The probabilities that the ratio of the between and within school variances is no greater than one. (Based on transformed data, i.e., log (parasite no. + 1.0).)

[2]The probabilities that the proportion of fish with more than the area median is the same for all schools.

[3]*** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; blank = $P > 0.05$.

Rate of Mixing of Schools

To estimate the rate of mixing of schools we needed to know the distribution of the parasites among schools before, and after, some known time interval. This we did not have for any of the Marquesas samples.

In New Zealand, however, some approximate calculations could be made because schools arrived from the tropics at different times. Sixteen of the 19 east New Zealand schools were of similar-sized fish and were all caught within 1 mo. These schools were divided into two groups: "early arrivals" and "recent arrivals". (This was done by ranking the schools using a combination of four parasites whose prevalences were positively correlated with each other, Nos. 16, 18, 19, and 20, and which were thought to be relatively short-lived parasites picked up in the tropics. Thus high numbers indicated a recently arrived school.) From catch data (Habib et al. 1980), we calculated that there was an average of 3 to 4 wk between the capture of 25% and 75% of the annual catch. This interval was taken as the approximate period between the arrival times of the early group and the recent group. If mixing was occurring, one would expect that the school-school differences for tropical parasites would be greater when the fish first arrived (the recent arrivals) than after they had been there for a few weeks (the early arrivals). However, this we could not demonstrate. Our sample sizes at this point were rather small (eight schools in each category), and in fact the reverse appeared to be the case, the early schools having a generally higher variability than the recent arrivals. This suggested that the early arrivals had come from several areas (and still had not fully mixed), whereas many of the later arrivals had perhaps come from one area.

DISCUSSION

Ten of the 26 parasites counted were species of didymozoid trematodes. These are almost exclusively a tropical group. Yamaguti (1970), for example, found 84 different species of didymozoid in fish around Hawaii. None were recorded in checklists of parasites from New Zealand (Hewitt and Hine 1972) or Canada (Margolis and Arthur 1979). Thus, although skipjack tuna are caught in both tropical and temperate waters, their didymozoid infections are evidently picked up primarily in the tropics.

Larval didymozoids have been found in small fish and in invertebrates. It is almost certain that the definitive host becomes infected by feeding on an infected intermediate host (Cable and Nahhas 1962; Nikolaeva 1965). In the tropics skipjack 40 to 60 cm in length feed largely on fish, squid, and stomatopods (Argue et al. 1983). In New Zealand, however, they feed almost exclusively on euphausids (Habib et al. 1980, 1981). This completely different diet in New Zealand, together with the fact that no endemic New Zealand fish are known to carry any didymozoids, lead us to the conclusion that few, if any, didymozoids are picked up in New Zealand waters.

The occurrence of 10 species of didymozoids in skipjack tuna caught in New Zealand, in numbers very similar to fish of the same size caught in the tropics, thus indicates that New Zealand and tropical fish were found until recently in a similar tropical environment. Almost certainly, the New Zealand fishery is based on fish that have recently migrated from the tropics, and not on fish recruited as postlarvae in temperate waters. This disagrees with tagging data which show that the bulk of New Zealand skipjack tuna of known origin were off New South Wales 10 mo earlier. However, the tagging inference is applicable to < 4% of the total New Zealand fish (Argue and Kearney 1983). Our conclusion is in agreement with Argue et al. (1983) who found no juvenile skipjack tuna in the stomachs of adults from

subtropical waters, though juveniles formed a significant component of the adult diet in the tropics.

The absence of degenerating *T. coryphaenae* and the positive correlation of parasite number and host length suggest that the parasite was long-lived and accumulated in the fish with age. The low numbers of *Tentacularia* in the 57+ cm fish caught in New Zealand indicate that these fish have had a different history from their peers in the tropics. The bulk of the skipjack tuna caught in New Zealand are 45 to 55 cm long. Less than 10% measure 60 cm or more (Habib et al. 1980, 1981). We have concluded above that the majority of New Zealand fish recently arrived from the tropics. The *T. coryphaenae* data indicate that the 57+ cm fish left the tropics at 45 to 55 cm long and have not returned. Evidently as fish age, they become less migratory. This was hypothesized by Kearney (1978).

Large fish were not necessarily permanent residents in New Zealand, however. Of 17 57+ cm fish on which full dissections were carried out, 2 were carrying the acanthocephalan *R. terebra*, a parasite thought to be relatively short-lived (see above) and not picked up in New Zealand. *Raorhynchus terebra* was common in fish from Norfolk Island (area H). Thus some of the large fish may have recently come from areas as far away as Norfolk Island.

The first two canonical variate analyses comparing all areas sampled suggested that fish 40 to 57 cm long had moved between areas and carried the longer lived parasites with them. Parasitologically, there was no evidence of more than one stock of skipjack tuna in the Pacific. Richardson (1983) observed an east-west cline in the gene frequency of two enzymes across the Pacific. From an analysis of 200 gene frequencies he proposed an "isolation by distance" model for skipjack tuna. In this, the degree of mixing of skipjack tuna genes was inversely proportional to the distance between the spawning areas. Tagging data have confirmed that there is some mixing of adult skipjack tuna in the central and western Pacific (Kleiber and Kearney 1983), though more than 95% of the tagged fish recovered during the SPC program were caught within 1,000 mi of their point of release (Kearney 1982).

Schools of skipjack tuna have been observed to break up when feeding (Forsberg 1980). This and observations from aircraft where schools have been seen to merge and later separate (Habib unpubl. obs.) have led to the hypothesis that skipjack tuna do not remain in a particular school for more than a day or so. Certainly the pattern of recovery of SPC tags suggested that tagged skipjack tuna underwent considerable mixing amongst schools soon after release (Argue and Kearney 1983). However, using Marquesas data we found that several parasites showed strong school associations, particularly didymozoid Nos. 19 and 20 (*D. intestinomuscularis* and *Lagenocystis/Univitellanulocystis* spp.). In another didymozoid, *Neometadidymozoon helicis* from the gills of *Platycephalus fuscus*, it takes up to a year for the worms to migrate through the tissues, pair up, mature, and die (Lester 1980). Though only a short migration is needed for didymozoids 19 and 20, as they are intestinal parasites, the worms are still likely to be in the skipjack tuna for a period of weeks. Thus, their strong association with particular schools suggests that school half-life is likely to be in terms of at least weeks rather than days.

In New Zealand, the large school-school differences observed in the numbers of *T. coryphaenae* and several other tropical parasites, especially in the early arrivals, indicate that at the time of catching, the New Zealand schools had not mixed sufficiently to mask their previously distinct tropical faunas.

Do schools remain intact for an extended period, perhaps for the life of the fish? Sharp (1978) found evidence of genetic similarity between individuals in core schools, suggesting that some members of the school were siblings. However, none of *L. multisacculatum*, *Coeliodidymocystis* sp., or *T. coryphaenae*, three long-lived parasites that showed significant school-school differences in New Zealand, showed any significant differences in the Marquesas. This suggests that within the probable long life of these parasites, fish caught in the Marquesas had changed schools and had thus obscured any patchiness in the distribution of the infective stages of the parasites. The parasitological data, then, do not support the hypothesis that fish stay in the same school for life.

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BEHAVIOR OF BOWHEAD WHALES, *BALAENA MYSTICETUS*, SUMMERING IN THE BEAUFORT SEA: A DESCRIPTION[1]

BERND WURSIG,[2] ELEANOR M. DORSEY,[3] MARK A. FRAKER,[4]
ROGER S. PAYNE,[3] AND W. JOHN RICHARDSON[5]

ABSTRACT

Behavior of bowhead whales summering in the Canadian Beaufort Sea was observed from an airplane and occasionally from shore during 1980-82, mainly during August. Behavior varied between years. In 1980, whales alternated periods of socializing with periods of feeding in several different ways: near the bottom (as evidenced by surfacing with mud), in the water column (suspected during long dives), and skim-feeding at the surface. In 1981, more time was spent apparently feeding in the water column, with some socializing and skim feeding. In 1982, almost all activity appeared to be feeding in the water column. In 1980, most whales studied were in water only 10-40 m deep. In 1981 they were farther from shore and in > 20 m depth, and in 1982 long (10-30 min) dives were common in depths of 40-600 m. Variability in distribution and behavior presumably was related to availability of prey.

Besides feeding and socializing, we saw sporadic bouts of aerial activity (breaches, tail slaps, etc.) and log play. During 1981 and 1982 we observed young-of-the-year calves apparently waiting at the surface while adults fed below. In 1982, two such lone calves played with debris in the water.

During near-surface skim feeding, whales often associated in V-shaped or echelon formations, with up to 14 animals staggered behind and to the side of each other, all moving in the same direction at the same speed, with mouths wide open. We hypothesize that such coordinated movement may increase the efficiency of feeding on concentrations of small invertebrates.

In recent years, much has been learned about behavior of several species of baleen whales (e.g., Payne 1983). Most long-term studies of whales have been carried out during winter, when social interactions, mating, and calving occur more often than feeding. Recently, however, detailed studies have been conducted in summer, when whales are primarily feeding (e.g., Dorsey 1983).

This paper describes the general behavior of bowhead whales, *Balaena mysticetus*, in the summers of 1980-82. A companion paper gives a quantitative description of the surfacing, respiration, and dive patterns (Würsig et al. 1984). This study was done to provide background data necessary to interpret observations of bowhead behavior in the presence of offshore industrial activities (Richardson et al. in press).

The Western Arctic population of bowheads winter in the Bering Sea, and migrate north and east to the eastern Beaufort Sea in spring. During summer (late June to early September), most are off northwestern Canada in Amundsen Gulf and the eastern part of the Beaufort Sea (Fig. 1). In the commercial whaling era in the 19th century, many bowheads apparently summered in the Chukchi and western Beaufort Seas off Alaska (Townsend 1935), but bowheads are no longer present in significant numbers off Alaska in summer (Dahlheim et al. 1980). The eastern Beaufort Sea is believed to be a major feeding area for bowheads (Fraker and Bockstoce 1980), but previous to 1980 there had been no comprehensive studies of bowheads in that area.

METHODS

Aerial Observations

We observed from a Britten-Norman[6] Islander aircraft based at Tuktoyaktuk (Fig. 1). The Islander has two piston engines, high wing configuration, and low

[1]This paper has been reviewed by the U.S. Minerals Management Service (MMS) and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of MMS, nor does mention of trade names or commercial products constitute MMS endorsement or recommendation for use.

[2]Moss Landing Marine Laboratories, P.O. Box 450, Moss Landing, CA 95039.

[3]New York Zoological Society, Weston Road, Lincoln, MA 01773; present address: Center for Long Term Research, Inc., Weston Road, Lincoln, MA 01773.

[4]LGL Ltd., Environmental Research Associates, 22 Fisher Street, King City, Ontario L0G 1K0, Canada; present address: Sohio Alaska Petroleum Co., Pouch 6-612, Anchorage, AK 99502.

[5]LGL Ltd., Environmental Research Associates, 22 Fisher Street, King City, Ontario L0G 1K0, Canada.

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[6] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

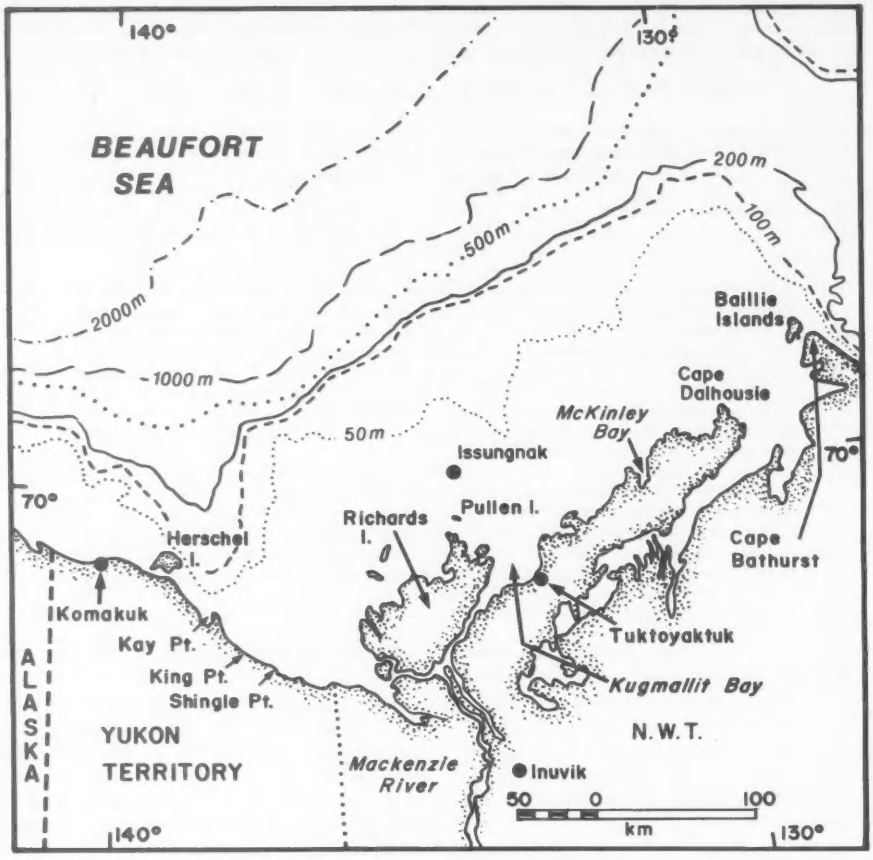

FIGURE 1.—The eastern Beaufort Sea.

stall speed. An OnTrac VLF/Omega navigation system indicated the latitude and longitude. A hand-held color video camera (JVC-CV-0001 in 1980 and 1981, Sony HVC-2000 in 1982) connected to a portable video cassette recorder (Sony SLO-340 in 1980 and 1981, Sony SL-2000 in 1982) was used through the side windows to record oblique views of bowheads.

Our usual strategy was to search until we encountered bowheads, and then circle over them as long as possible while making observations. If contact was lost, we searched for another group. We created a fixed reference point about which to circle when bowheads were below the surface by dropping a fluorescein dye marker. Near the start of most periods of circling above whales, a sonobuoy (AN/SSQ-41B or AN/SSQ-57A) was dropped to broadcast underwater sounds to the aircraft, where they were recorded.

In 1980-82, we flew for a total of 340 h during 71 offshore flights. Of this time, we circled over bowheads for 97.7 h during 46 flights. Flight duration was typically 4-5.5 h. Flights were made between 3 and 31 August 1980, 31 July and 8 September 1981, and 1 and 31 August 1982. We encountered bowhead whales during every day we flew in 1980, and during the majority of days in 1981 and 1982.

We usually did not fly when wind speed exceeded 25 km/h; in more severe conditions whales are difficult to detect and behavior cannot be observed reliably. While searching for whales, we usually flew at 457-610 m (1,500-2,000 ft) above sea level (ASL),

and at 185 km/h. While circling over whales, we reduced speed to 148 km/h. Bowheads rarely appeared to be disturbed by the aircraft when it remained at or above 457 m (Richardson et al. in press).

The aircraft crew usually consisted of four biologists and the pilot. Three biologists were seated on the right side of the aircraft, which circled clockwise during behavioral observations. Biologists seated in the right front (copilot's) seat and in the seat directly behind it described behaviors. These descriptions were recorded onto audiotape, onto the audio channel of the video recorder, and, in 1981, directly onto data sheets by a biologist in the left rear seat. The biologists in rear seats videotaped whales, handled sonobuoys, and kept records. All personnel on board were in constant communication through an intercom.

While circling bowheads, we usually were able to obtain consistent records of 12 variables and types of behavior:

1) Location of sighting (and, therefore, water depth);
2) Time of day;
3) Individually distinguishing features, if any, on whales;
4) Number of individuals visible in area and number of calves;
5) Headings and turns of each whale in degrees true;
6) Distances between individuals (estimated in whale lengths);
7) Length of time at surface, and sometimes length of dive;
8) Timing and number of respirations or blows, including underwater blows;
9) Possible indications of feeding: mouth open, defecation, mud streaming from mouth;
10) Socializing, possible mating, probable nursing by calves;
11) Aerial activity: breaches, tail slaps, flipper slaps, lunges, rolls;
12) Type of dive: flukes out, peduncle arch, predive flex.

Descriptions of these behaviors appear later.

In most parts of this paper we consider only the observations under "presumably undisturbed" conditions. Bowheads were considered "potentially disturbed" if our aircraft was at < 457 m ASL, if a boat was underway within 4 km, or if sonobuoys showed that industrial noise was readily detectable in the water. The "presumably undisturbed" behavioral observations were distributed by hour of day and water depth as presented in Figures 2 and 3.

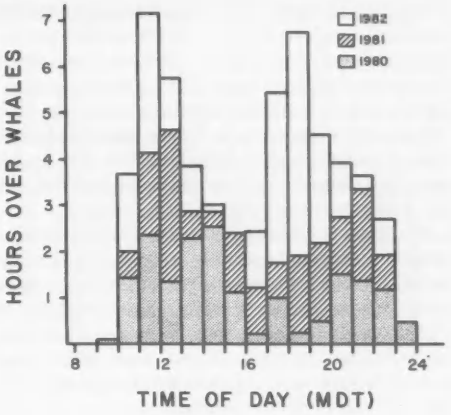

FIGURE 2. – Hourly distribution of behavioral observation time from the air of bowhead whales.

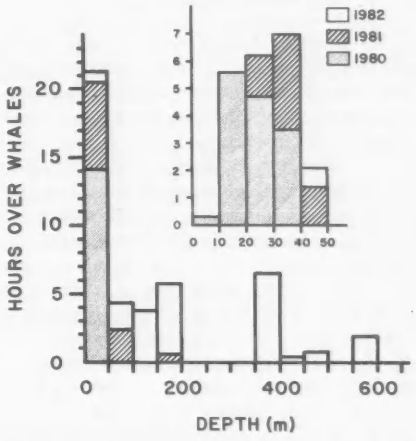

FIGURE 3. – Distribution of behavioral observation time from the air by depth of water of bowhead whales. The inset shows effort for the 0-50 m range by 10 m intervals.

Shore-Based Observations

Shore-based observations were obtained in 1980 and 1981 from the east end of Herschel Island, Yukon (lat. 69°35'N, long. 138°51'W), and about 225 km west of Tuktoyaktuk (Fig. 1). A surveyor's theodolite was used from a high point (50 m ASL in 1980,

90 m ASL in 1981) on the coast. We used a Wild T1 theodolite with 6-s accuracy and 30-power optics in 1980, and a Nikon NT-2A with 20-s accuracy and 30-power optics in 1981. Horizontal and vertical bearings were later translated to x and y map coordinates. This transiting technique, developed by R. Payne, is described by Würsig (1978). The station was in use from 19 August to 1 September 1980, and 23 August to 13 September 1981.

Locations of most whales within a 10 km radius of the theodolite station during fair weather and daylight hours were documented. Unfortunately, whales rarely approached Herschel Island closer than 5 km during the 1980 field season, so details of behavior were difficult to discern. In 1981, fewer whales were seen, but they were closer to shore, allowing more detailed behavioral observations.

RESULTS

The Surfacing-Dive Cycle

In the Beaufort Sea in summer, nonmigrating bowhead whales typically alternate between dives of variable length, depending on activity, and surfacings within which there are several respirations. This pattern differs slightly from that during migration, when sounding dives (around 15 min long) are separated by periods when several brief surfacings, each with a single respiration, alternate with "series" dives about 15 s long (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). Presumably, migrating animals dive between respirations to avoid hydrodynamic drag imposed by the air-water interface. No such submergence is necessary for a whale that is not moving rapidly through the water. However, the basic repertoire of breathing several times in relatively, closely spaced series and then not breathing for many minutes (during the long dive) is similar during both prolonged directed movement and more stationary activity. The pattern extends to some degree even to whales that remain at the surface for long periods (up to 30 min or more during surface skim feeding, socializing, or play). They generally breathe several times within a few minutes, and then cease breathing for a longer time, despite their near proximity to the surface and the availability of air. Similar patterns are seen in other whales, including right whales, *Eubalaena glacialis*, (Kraus et al. 1982) and gray whales, *Eschrichtius robustus*, (Sumich 1983). Durations of surfacings and dives, intervals between successive blows, and number of blows per surfacing are described in Würsig et al. (1984).

Surfacing and Respiring

Whales in water deeper than about 30-45 m usually surface head and blowhole first after a sounding dive, with the body oriented at some angle (such as 30°) from horizontal. When whales do not dive very deeply (as in shallow water), the surfacing is less due to active swimming upward, and the head and tail surface at approximately the same time.

A blow is an exhalation of air by a whale. Blows can occur above or below the surface. Surface blows are usually visible as a white cloud of water spray, but may be so weak as to be undetectable. The first blow after a surfacing usually appears strong, probably because it is a more forceful exhalation and because water is present above the blowholes during or just after surfacing. On calm days and when whales lie at the surface with the blowholes exposed, the blowholes are relatively dry, and blows may be difficult to detect. Blows of calves can also be difficult to see.

Surface exhalations of gray; humpback, *Megaptera novaeangliae*; fin, *Balaenoptera physalus*; and southern right whales, *Eubalaena australis*, are almost always followed immediately by an inhalation (B. Würsig, pers. obs.). Hence we suspect, following Scoresby (1820), that exhalations and inhalations generally occur together in bowhead whales as well.

Diving and Associated Behavior

The predive flex is a distinctive concave bending of the back seen several seconds before many dives. The whale flexes its back by about 0.5-1 m, so that the snout and tail disrupt the surface. Considerable white water is created at these two points. The whale then straightens its back and lies momentarily still before arching the back convexly as it begins its roll forward and down. The predive flex is seen from low vantage points as an abrupt lifting of the head, because the flukes apparently only touch the water surface from below.

The predive flex was seen more often during 1980 than during 1981 or 1982. Although it occurred previous to dives well over 50% of the time in 1980, it occurred in only 8% of the observations (before 29 of 352 dives) in 1981. For 1982, we have especially detailed analyses of predive flexes. In that year, predive flexes occurred in presumably undisturbed noncalves before 32 of 132 dives (24.2%); flexes occurred more often in late August than earlier (Table 1). Dives following predive flexes were, on the average, about twice as long as dives without predive flexes (19.00 ± SD 7.877 min, n = 13, vs. 10.15 ±

TABLE 1.—Dives preceded by a predive flex among noncalf bowheads early and late August 1982. The frequency of occurrence is significantly higher after 19 August (chi-square = 4.29, df = 1, $0.025 < P < 0.05$).

	Up to 19 Aug. 1982	After 19 Aug. 1982	Total
Dives with predive flex	9	23	32
Dives without predive flex	49	51	100
Total	58	74	132

7.465 min, $n = 36$; Mann-Whitney U = 97.5, $P < 0.01$). Five dives were preceded by two predive flexes, with the flexes separated by a blow. Two dives were preceded by three flexes. We have no data on durations of dives following multiple flexes.

During the dive, which can at times be predicted by the predive flex, the whale makes its body convex and pitches forward and down. If the angle of submergence is steep, the tail is usually raised above the surface; if not, the tail may remain below or just touch the surface. Rarely do bowheads sink down without visibly arching the back.

In 1982, 59 of 138 dives (42.8%) were preceded by raised flukes. Of the 32 dives preceded by one or more predive flexes, 21 also showed raised flukes. These two predive behaviors tended to occur together ($\chi^2 = 3.94$, $P < 0.05$, df = 1), and dives with raised flukes were significantly longer than those not preceded by raised flukes (18.67 ± SD 9.966 min, $n = 12$, vs. 10.05 ± 6.956 min, $n = 38$; Mann-Whitney U = 114, $P < 0.01$).

There was no difference in durations of surfacings concluded with and without raised flukes. However, surfacings including predive flexes tended to be longer than those without predive flexes (3.09 ± SD 1.038 min, $n = 14$, vs. 1.79 ± 1.284 min, $n = 52$; $t = 3.50$, df = 64, $P < 0.001$), probably because durations of surfacings and dives are correlated (Würsig et al. 1984).

The function of the predive flex is unknown. Flexes occur more often before longer dives (which may take the whales deeper in the water column). Raising the flukes before a dive appears related to the steepness of the dive; whales that roll forward while dropping the front of the body at least 30° below the water surface usually raise their flukes. The weight of the raised tail stock in the air must help propel the animal downward (much as human skin divers raise their legs above the surface during the initiation of a steep dive). Although raised flukes are common during steep dives in many whales, the predive flex has not been reported in other species.

The Underwater Blow

The underwater blow is a burst of air emitted underwater. The bubble burst is circular and up to 15 m in diameter when it arrives at the surface. Release of air underwater was recorded about 10 times via nearby (< 1 km away) sonobuoys; the noise was detectable for 3-4 s, but the white water and expanding concentric wave were visible much longer. On one occasion, we definitely saw that the air came from the blowhole rather than the mouth, and we believe that this is always true. We saw underwater blows immediately after whales dove and just before they surfaced, but more usually in the middle of the dive, when the whales were out of sight.

Underwater blows were most frequent in 1980 during periods of pronounced feeding in water < 14 m deep (see Feeding section). In 1980, we saw 158 underwater blows in 30.4 observation hours; in 1981, 57 blows in 30.8 observations hours; and in 1982, only 6 blows in 36.5 observation hours. (The difference between years is statistically significant; $\chi^2 = 189$, df = 2, $P < 0.001$.) Concurrently, whales tended to be found in progressively deeper water from 1980 to 1982.

Underwater blowing occurred more often in the morning and evening than around solar midday in both 1980 and 1981 (Fig. 4; solar noon occurs about 1500 MDT in the eastern Beaufort Sea). The midday "lull" in underwater blowing coincided with a peak in frequency of socializing, the main nonfeeding behavior observed (see Social Behavior section below). Nemoto (1970) suggested that baleen whales in general show a high level of feeding activity in the

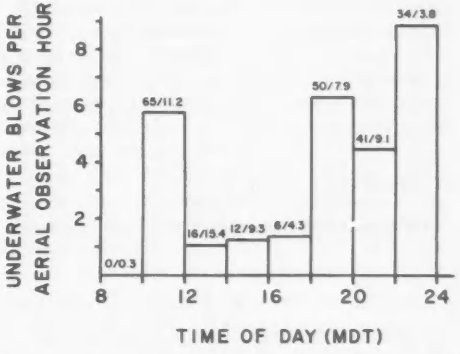

FIGURE 4.—Number of underwater bowhead whale blows per aerial observation hour in relation to time of day, 1980 and 1981 combined. There were few underwater blows in 1982. The numbers at the top of each column are number of blows seen/number of observation hours.

morning and a lower level during midday, but we have no direct evidence of this in bowheads.

Although underwater blows seem to occur more often in shallow water when whales may be feeding, we have not included this behavior as a definite part of feeding. There is only a general similarity to bursts of bubbles associated with feeding humpback whales in the North Atlantic (Hain et al. 1982), and the bubble nets reported for humpbacks by Jurasz and Jurasz (1979) are very different.

Social Behavior

Behavior was termed social when whales appeared to be pushing, nudging, or chasing each other, or when they were within half a body length of one another. Whales within half a body length almost always stayed close to each other, and oriented towards each other or interacted in some manner. Thus, our use of proximity as an indication of sociality was appropriate. Interactions between mothers and calves, and between whales skim feeding in close proximity, were not included as social interactions in this analysis. Whales may, of course, communicate by sound, and thus may socialize over far greater distances than those described here. Our sonobuoys often detected bowhead calls while socializing was underway. However, we could not verify whether acoustic communication was occurring between any particular whales, so we restricted our definition of socializing to visible behavior. Synchronous diving and surfacing over areas many kilometers in diameter (see below) may represent a different form of social interaction from what we discuss in this section. Because groups of whales usually could not be reidentified positively from one dive to the next, we treated observations of social behavior at intervals of > 5 min as independent for the purpose of counting number of interactions. Conversely, we did not score social behavior by one group more than once in 5 min when counting frequency.

Frequency of Socializing

Social behavior was seen less frequently in late August-early September than in early August, both in 1980 and 1981 (Table 2). Rugh and Cubbage (1980) and Carroll and Smithhisler (1980) reported a higher incidence of social interactions during the spring migration around Alaska than we saw at any time. The apparent waning of social activity from early to late August may be part of a continuing decrease from a higher level in spring.

Little socializing was observed in 1982. In presumably undisturbed whales, we observed only seven cases, all on 8, 19, and 23 August. Throughout August 1982, most whales were alone and making long dives. The overall socializing rate for each year (Table 2) demonstrates the dramatic decrease in socializing in 1982 compared with the two previous years. This decrease may be related to the increase in 1982 in the average distance from shore and depth of water at locations where bowheads were studied. However, we found no consistent trend for socializing to occur more often in shallow water than in deep water within 1 yr.

There was some indication of hour-to-hour variation in amount of social activity in all 3 yr (Fig. 5). In 1980 and 1981, it peaked around 1400-1600 MDT, the noon period by sun time. In 1982, the few (7) cases were recorded from 1600 to 2000 MDT, somewhat after solar noon (Fig. 5). In both 1980 and 1981, there was another peak after 2000 MDT. Why whales should engage in more social activity around noon (and possibly in the evening) than at other times is unknown. However, diel rhythms are well known in several mammals (e.g., Saayman et al. 1973 for bottlenose dolphins; Matsushita 1955 for sperm whales; Schevill and Backus 1960 for humpback whales). The increased level of socializing around noon may reflect a lowered level of feeding at that time, which Nemoto (1970) suggested for baleen whales in general.

Physical Interactions

During surface interactions with nearby whales, socializing whales often turned. In contrast, nonsocializing whales often surfaced and dove again without changing direction. In the 3 yr, turns oc-

TABLE 2.—Number of social interactions per aerial observation hour, divided into about 10-d periods, in 1980, 1981, and 1982. Only presumably undisturbed periods are included.

Year	1-10 Aug.	11-20 Aug.	21-31 Aug.	1-10 Sept.	Overall
1980	28/7.0 = 4.0	6/2.9 = 2.1	8/7.7 = 1.0	—	42/17.6 = 2.4
1981	14/4.3 = 3.3	12/5.5 = 2.2	9/3.3 = 2.7	4/4.0 = 1.0	39/17.1 = 2.3
1982	1/1.5 = 0.7	3/7.6 = 0.4	3/12.8 = 0.2	—	7/21.9 = 0.3

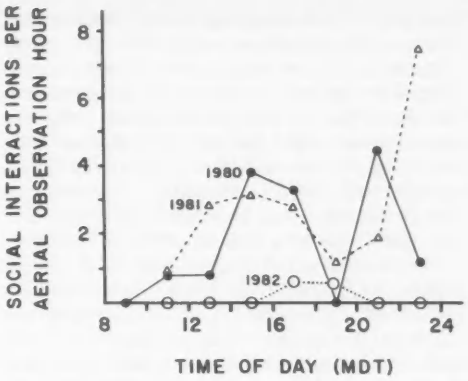

FIGURE 5. – Number of bowhead whale social interactions per aerial observation hour in relation to time of day.

curred during 53 of 133 (40%) surfacings with socializing, and in 128 of 484 (26%) without socializing ($\chi^2 = 9.04$; df = 1, $P < 0.005$).

When bowhead whales touched, they often appeared to push each other. Pushing or touching was usually done with the head, while oriented head to head, or head to tail. However, we also saw whales of adult size dive under the bellies of other whales and apparently nudge or push the other whales near their genital areas. At other times, whales dove under each other at very close range without any indication that they were touching.

Apparent chase sequences involved two or three whales in a line, usually < 2 body lengths apart. During these chases one whale often turned abruptly left or right, and the second (and third) followed. Movement was faster during chases than at all other times when we saw presumably undisturbed whales at the surface.

Both touching and chasing may at times represent low levels of sexual activity, but this is unproven because we cannot determine the sex of a bowhead whale from a distance. Payne and Dorsey (1983) and Tyack and Whitehead (1983) described physically interacting right and humpback whales, respectively, which appeared to be engaging in social-sexual activity.

Possible Mating

In 1981, we twice observed apparent mating. The more prolonged observation was on 10 August 1981, within a 25 km^2 area where there were 20-30 whales whose main activity was socializing. Two whales interacted for over 1 h with chases, flipper caresses, belly-to-belly orientation, rolls toward and away from each other, head nudges to the genital area and to the rest of the body, tail slaps, and flipper slaps. One whale, a recognizable animal that we termed "Whitespot", was about 1-2 m longer than the other ("B") and was the more aggressive. Although B originally nudged the genital area of Whitespot, it was Whitespot who appeared to initiate flipper caressing and rolls toward B. The two whales rolled their ventral surfaces together for about 5 s, but B then rolled its ventrum in the air in an apparent attempt to avoid ventral contact with the larger animal. As it rolled away from Whitespot, B defecated, and when Whitespot moved its head toward the genital area of B, B defecated two more times in rapid succession. B then dove away from Whitespot, and Whitespot followed it at the surface in an apparent chase. Whitespot then stopped and, alone at the surface, rolled two times and tail slapped while on its back. It then dove, and the two appeared together again at the surface 4 min later, with no further energetic surface interaction.

We do not know the sex of either animal, but it appeared that Whitespot was attempting to copulate with the reluctant animal. Some of us (Würsig and Payne) have observed southern right whale females frequently roll their ventra away from aggressive males, leaving their genital areas above the surface of the water, where the males cannot reach them. Everitt and Krogman (1979) photographed very similar behavior of a group of six bowheads off Barrow, AK, in May. Our observations here were highly reminiscent of such behavior. Although adult females are slightly larger than adult males in both right and bowhead whales, we commonly see large southern right whale males in pursuit of smaller females, which attempt to avoid the males.

On 25 August 1981, two bowheads briefly placed their ventral surfaces together and clasped each other with their flippers. After 1 min, they rolled apart, blew, and dove slowly as a third whale approached. The mutual rolling and leisurely diving indicated that, if this was copulatory behavior, it was mutually undertaken by the two whales in contrast to the previous example.

Group Structure and Stability

Two observations of recognizable bowheads provided evidence about group structure and stability. We observed a distinctively marked pair of adults, one accompanied by a calf, at about lat. 70°10′N, long. 133°50′W on 7 August 1980. We saw a similar-

ly marked group of two adults and a calf, almost certainly the same whales, on 20 August at lat. 70°07'N, long. 131°30'W, which is about 85 km from the place they had been seen 2 wk earlier. This observation suggests that some groups of bowheads are maintained for at least a few weeks. The observation also suggests that females with calves may sometimes be accompanied by escorts, as has been observed for wintering humpback whales (Herman and Antinoja 1977).

Feeding

Feeding appeared to occupy much of the time of the bowheads that we observed, but we had to rely on indirect clues, such as observations of swimming with open mouth, mud streaming from the mouth, or presence of feces in the water, to indicate that feeding had taken place. The four possible types of feeding behavior that we identified were 1) water-column feeding; 2) near-bottom feeding; 3) skim feeding; and 4) mud tracking. Of these, the first three rather clearly represented feeding, whereas the function of the last was less certain. As noted above, underwater blowing showed some association with feeding, but the connection was uncertain.

In 1980, certain feeding behaviors occurred in particular areas: only water-column feeding was seen near the Issungnak artificial island site (Fig. 1), whereas only skim-feeding was seen off the Tuktoyaktuk Peninsula near McKinley Bay. In 1981, there was less evidence for feeding, although we suspect that most feeding occurred in the water column. In 1982, when whales dove for long periods (up to 30 min), we suspected water-column feeding to be occurring at almost all times.

Water-Column Feeding

Water-column feeding could not be observed directly. Whales were scored as feeding in the water column when they dove for long periods, and when, between long dives, there was much defecation and only slow forward motion. Defecation is simply an indication of prior feeding. However, particular behaviors such as a series of long dives usually continued for many hours, so occurrence of defecations between long dives was considered indicative of ongoing feeding in the water column.

The frequency of apparent water-column feeding was not constant. In 1980, we saw bowheads water-column feeding from 3 to 22 August. Thereafter, few whales were present in the area where we had observed this behavior, and whales seen elsewhere did not seem to feed in the water column. In 1981, when we saw less defecation, we only scored as water-column feeding some adult whales that dove for prolonged periods on 24 August, while calves remained at the surface. In 1982, most whales made long dives. These whales probably were feeding in the water column, even though we saw little defecation at the surface. Feeding below the surface may have occurred during many other dives besides those that we classified as dives with water-column feeding.

Observations on 3 August 1980 typify water-column feeding behavior. On this date, bowheads were north of Kugmallit Bay where water depth was 18-38 m. The surface water was turbid, brackish water from the Mackenzie River, but beneath this surface layer, there was a second layer of clearer, saline Beaufort Sea water (Griffiths and Buchanan[7]). The whales occurred in groups of 2-10 animals, and occasionally as individuals without others nearby. Group members showed a high degree of synchrony, often surfacing very close together and remaining close at least until they dived again. Not only did the members of a group surface and dive synchronously, but various groups spread over an area several kilometers in diameter all tended to be at the surface or beneath it at the same time.

While the animals were at the surface, they moved slowly forward while taking a series of breaths. As each individual dived, it raised its tail clear of the water, and disappeared from view in the turbid water. Thus, these dives must have taken the whales well below the surface. When the whales were at the surface, they often disturbed the turbid surface layer, exposing dark patches of seawater from deeper depths. However, while submerged after a dive that was preceded by raised flukes, they did not affect the thin surface layer, indicating that they were probably feeding in the underlying clearer ocean water. Defecation was frequent, suggesting that feeding may have taken place recently. The feces clouds were red-orange.

Bottom Feeding

On 12 August 1980, we noticed clouds of mud suspended in the water about 25 km west of Issung-

[7]Griffiths, W. B., and R. A. Bachanan. 1982. Characteristics of bowhead feeding areas. *In* W. J. Richardson (editor), Behavior, disturbance responses and feeding of bowhead whales *Balaena mysticetus* in the Beaufort Sea, 1980-81, p. 347-455. Unpubl. Rep., 456 p. LGL Ecological Research Associates, Inc., Bryan, TX, for Bureau of Land Management, U.S. Department of the Interior, Washington, DC. Available from Minerals Management Service Alaska OCS Region, P.O. Box 101159, Anchorage, AK 99510.

nak artificial island (Fig. 1). The clouds represented suspended mud and not plankton because the material was of the same color as mud dredged up by industrial activities. Whales surfaced with large amounts of muddy water streaming from their mouths, indicating they had been feeding from or near the bottom. This behavior occurred in 24-29 m of water and seemed very localized. We saw no indication of bottom feeding in the same area on 22 August 1980, but we had observed similar mud clouds nearby on 9 August, when prolonged observations were not possible. On 25 August 1981, whales again surfaced with mud streaming from their mouths. The location was 15 km south of the position where we observed such behavior in 1980; water depth was only 10-13 m.

These are, to our knowledge, the first published behavioral observations of apparent near-bottom feeding by bowhead whales. However, Johnson et al. (1966), Durham (1972), and Lowry and Burns (1980) detected pebbles and bottom-dwelling species in bowhead stomachs.

Bottom-feeding whales were usually separated from other whales by 150-300 m when at the surface. On 12 August 1980, at least 10 whales were bottom feeding within an area of 3 km radius. Whether they were feeding on inbenthic or epibenthic invertebrates we do not know. In the eastern Beaufort Sea, the average biomass of inbenthic animals greatly exceeds that of epibenthic animals (Griffiths and Buchanan footnote 7). However, the latter may occur in dense swarms in certain places. For a balaenid whale, such swarms would seem to be a much more suitable type of food than inbenthic organisms. Mud might be taken inadvertently along with epibenthic animals.

Skim Feeding

The only feeding type that we observed directly was skim feeding. In the third week of August 1980, we observed whales moving slowly and deliberately at the surface with their mouths open wide. Usually the rostrum just broke the surface of the water, and was parallel to it. In these cases, the lower jaw was dropped to varying degrees, as could be seen from the depth of the white chin patch. In 1980, skim feeding was observed along the Tuktoyaktuk Peninsula in water 12-22 m deep. Whales occasionally skim fed alone, but more often did so in groups of 2-10 or more individuals. During any one observation period, they stayed in the same general area by repeatedly turning and did not appear to make any net geographic movement. However, we found groups of skim-feeding whales in different locations on different days.

During 1981, we witnessed skim feeding on a large scale only on the evening of 18 August, 32 km NNW of Pullen Island in water 25 m deep. About 20-30 whales in the 25 km^2 area were swimming with mouths open; they travelled slowly, usually just below the surface ($\sim$ 2-3 m deep). Copepods were unusually abundant in near-surface waters at this location and time (Griffiths and Buchanan footnote 7). On 23 and 24 August 1981, we saw one isolated example on each day of a whale feeding at the surface briefly (observed for < 1 min) in approximately the same area as on 18 August.

Typically, skim-feeding whales were oriented with their backs at the water's surface. However, they occasionally swam on their sides with mouths open at an angle of about 60°, and once we saw two whales separated by three body widths swimming on their sides, belly to back. In one instance, a skim-feeding whale swam inverted for at least 3 min, with the underside of its chin at the surface.

Frequently, the skim-feeding whales swam in echelon formation, each whale swimming just behind the preceding whale, but offset laterally by one-half to three body widths, reminiscent of geese in V formation (Fig. 6). At other times, they swam abreast and parallel to one another. Videotape from 18 August 1981 showed that whales within the echelons were a mean of 0.53 whale lengths apart (SD = 0.599, $n = 66$), or about 8 m. These distances were measured from different echelons or from the same echelon at intervals of at least 5 min. We videotaped a recognizable whale for almost 3 h on this day as it skim fed in changing echelon formations, usually taking the lead position. Echelons were clearly dynamic in terms of membership, size, and organization. In 1981, the mean echelon size was 4.7 animals (SD = 4.05, $n = 23$). While the largest such formation observed in 1980 contained 5 individuals, the largest in 1981 contained 14 animals.

We suspect that echelon feeding increases the feeding efficiency of those animals staggered behind and to the side of other individuals, perhaps by helping them to catch prey that escape or spill from the mouth of the whale in front, or by reducing the ability of prey to escape to the side. Skim feeding in echelon may allow more effective exploitation of concentrated patches of small prey than would be possible if whales were feeding alone. If so, the change in efficiency that accrues when echelons are formed may have an important cost/benefit effect on energy expended per whale. The predominant prey types of bowheads include copepods and euphausiids (Lowry

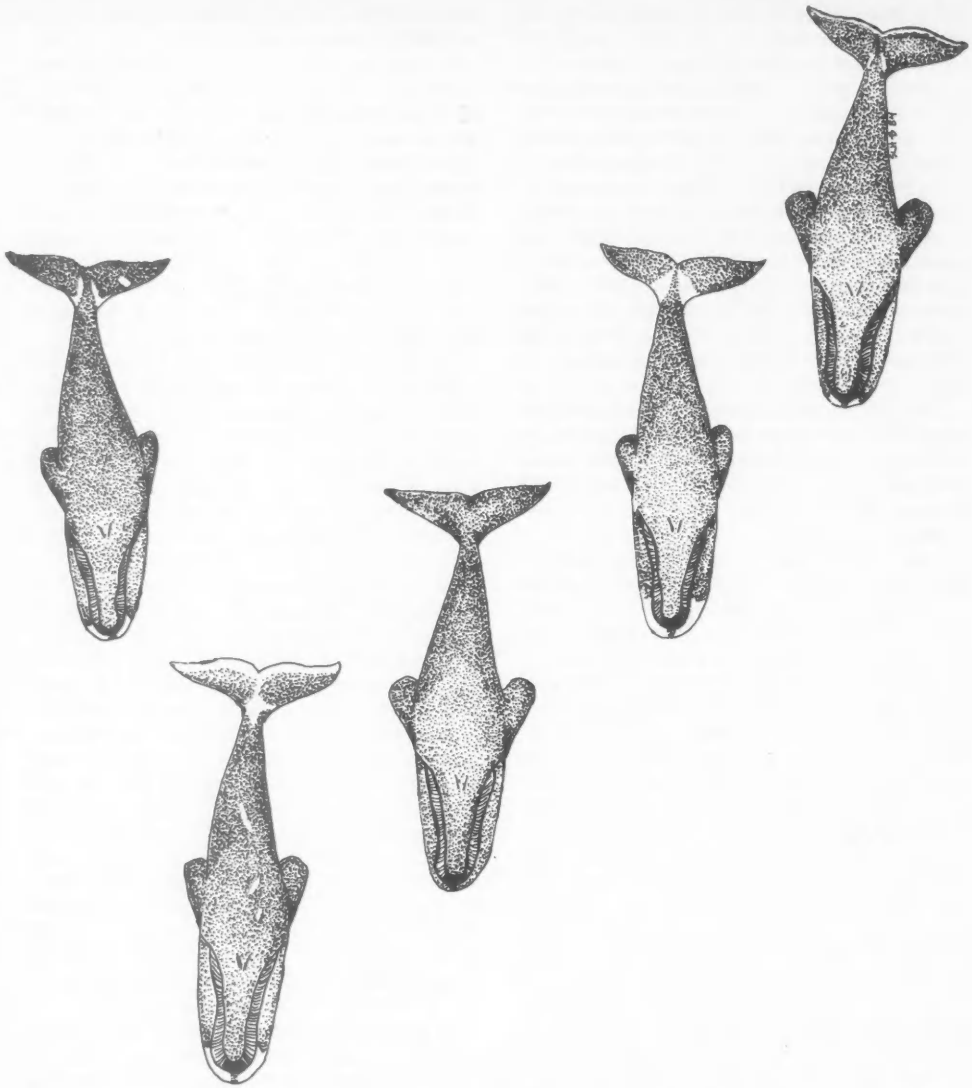

FIGURE 6. – Five bowhead whales skim feeding in echelon formation. Drawing after a 35 mm photograph and video footage from the air.

and Burns 1980). The latter are adept at avoiding most sampling gear because of their rapid movement. However, bowheads at times collect euphausiids in very large numbers, despite the bowhead's slow swimming speeds relative to the better known euphausiid predators such as rorquals. Perhaps echelon feeding is especially helpful in catching fast-swimming prey such as euphausiids.

During 1982, little direct evidence for feeding was noted. We saw no skim feeding at the surface, and noticed only nine isolated instances when a whale's mouth appeared to be open slightly. These brief, slight

openings of the mouth contrasted sharply with the sustained large gapes observed in 1980 and 1981, and probably did not represent feeding. In southern right whales, Payne (pers. obs.) has observed mouth opening that he interprets as yawning following sleep.

Mud Tracking

Mud tracking occurred when whales swimming in shallow water (< 12 m depth) disturbed the bottom sediments with each fluke beat, producing clouds of mud joined by a narrower trail of muddy water. These elongated clouds of mud were different from mud clouds produced during presumed bottom feeding. Although we often could not see the whales, in at least a few instances their mouths were open. We saw mud tracking during only three flights in the third week of August 1980.

Mud tracking probably represented incidental disturbance of bottom sediments by a whale feeding near the bottom in shallow water. We saw no evidence that bowheads ever turned and swam back along a mud track made previously. The mud tracks tended to be straight, and some extended for well over 1 km. At certain times, clouds of mud streamed from the whale's body as it swam near the surface. In this case, we suspect that the whales had contacted the bottom, and that the mud had stuck to their bodies. Sometimes, mud-tracking whales exhaled while submerged, producing a characteristic burst of bubbles (see section on The Underwater Blow).

Defecation

Defecation usually was evident as a cloud (2-3 m diameter) of red-orange feces near the surface. Whales almost invariably were moving forward or diving when they defecated, and over 50% of the bowheads observed defecating in 1980 did so while the tail was arched up high out of the water just before the dive. The anus was thus close to or at the surface. No part of the body appeared to touch the feces cloud, which was visible at the surface for up to 10 min. When whales moved forward while defecating, the feces were more dispersed and disappeared within 1-2 min. Brown (1868) noted that feces of eastern arctic bowheads were also red. Renaud and Davis[8] observed red clouds of feces off the Tuktoyaktuk Peninsula in 1980.

Defecation was seen more often in 1980 (23 cases during 30.4 h over whales) than in 1981 (11 cases during 30.8 h over whales). The difference is statistically significant ($\chi^2 = 4.39$, df = 1, $0.025 < P < 0.05$), and may be related to year-to-year differences in feeding patterns. In 1982, we saw only one defecation (by a lone whale playing with a log). Because we can only observe defecations by whales at the surface, we compared the rates in reference to the number of whale-hours of observation at the surface. In 1980, there were 2.29 defecations/whale-hour at the surface, as opposed to 0.73 in 1981, and 0.09 in 1982 ($\chi^2 = 27.58$, df = 2, $P < 0.001$). This decrease could result either from decreased defecation (indicative of less feeding), or from an increasing tendency to defecate under the surface where we could not observe it. During 1982, dives were longer than in the 2 previous years (Würsig et al. 1984), and we suspect that much water-column feeding was taking place.

Adult-Calf Pairs

Calves of the year are a light tan color, distinct from the dark black of noncalf bowheads. An adult that remained close to a calf was assumed to be the calf's mother. For the closely related southern right whale in winter, Payne and Dorsey (1983) found that in unambiguous adult-calf pairs, the adult was always a female, and that identified calves were always seen with the same individually identified female. At times, we saw apparent nursing as calves submerged briefly, oriented toward the teat region of the adult. In 1982, we made longer observations of calves than in either 1980 or 1981.

The relative lengths of six calves measured from videotape sequences recorded during August 1981 were a mean of 0.57 ± SD 0.052 adult body lengths. Many of the calves we observed in August 1982 appeared to be smaller, about one-third adult size. This is corroborated by the fact that 14 calves measured via photogrammetry in August-early September 1982 were 4.1-7.6 m long, or 33-45% (mean 41%) of the length of the accompanying adult (Davis et al.[9]). It may be that births occurred earlier in the year in 1981 than in 1982, or that the females videotaped in 1981 were smaller, on average, than those measured in 1982.

[8]Renaud, W. E., and R. A. Davis. 1981. Aerial surveys of bowhead whales and other marine mammals off the Tuktoyaktuk Peninsula, N.W.T., August-September 1980. Unpubl. Rep., 55 p. LGL Ltd., Toronto, for Dome Petroleum Ltd., Box 200, Calgary, Alberta T2P 2H8, Canada.

[9]Davis, R. A., W. R. Koski, and G. W. Miller. 1983. Preliminary assessment of the length-frequency distribution and gross annual reproductive rate of the western arctic bowhead whale as determined with low-level aerial photography, with comments on life history. Unpubl. Rep., 91 p. LGL Ltd., Toronto, for National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115.

When an adult and calf were both at the surface, they were usually within one adult-length of each other. Videotape sequences showed the mean distance apart to be 0.61 adult whale lengths (SD = 0.564, n = 8, range = 0.1-1.5), or about 9 m. The calves spent most of the time lying beside the adult, and facing in the same direction as the adult. At times, the calf strayed up to two whale lengths from the adult, and then oriented toward the adult. While the adult lay at the surface, the calf often submerged near the belly of the adult with its tail close to the adult's tail. This position is probably indicative of nursing. The calf then often swam under the adult, surfaced on the other side, respired one or two times, and submerged again toward the adult's belly, alternating sides with each surfacing. The calf also appeared at times to rest, lying quietly on the back and tail of the adult.

Calves were sighted at similar frequencies in all 3 yr (Table 3). However, durations of surfacings by calves were longer in 1982 than in 1980-81. Because of this, calves accounted for 15% of whale-hours of observation in 1982, but only 3% in 1981, and 4% in 1980 (Table 3).

Calves Alone

In 1982, calves spent almost 40% of their time at the surface unaccompanied by an adult. This was comparable with their behavior in 1981, but unlike 1980 when they were rarely seen alone. (Table 3).

On 24 August 1981, we saw three calves separated from each other and from the closest adults by 100 m to more than 300 m. It was, therefore, often not possible to assign calves to particular females. The nearest adults spent much time submerged, but the calves remained stationary at the surface. At one point, we videotaped an adult that surfaced 4.9 adult lengths from a calf lying stationary at the surface. During another videotaped sequence, an adult-calf pair, 0.2 lengths apart, was separated from a lone calf by 7.6 adult lengths. We suspect that the adults were feeding in the water column while calves waited at the surface.

In 1982, we observed four lone calves at the surface, on 18, 19, and 23 August, and on three of these occasions we saw the calf rejoin its presumed mother. On 18 August, a lone calf surfaced and oriented straight toward an adult at a distance of 1.6 km. When it came within 75 m of the adult, the adult also began to swim rapidly toward the calf. During a second incident on the same day, a calf and adult swam rapidly toward each other from at least 300 m distance. In both cases, the two dove simultaneously after coming together. On 23 August 1982, an adult surfaced 180 m from a lone calf, and the adult oriented toward the calf. When the two whales were ~ 120 m apart, the calf also oriented toward the adult, but the adult was mainly responsible for closing the distance between them, as it swam at medium speed toward the calf. When the two whales were ~ 20 m apart, the calf dove and reappeared 18 s later, reoriented by 180°, lying to the right of the adult, and facing in its direction. The calf then

TABLE 3.—Calf sightings and observation time in 1980, 1981, and 1982. Only flights with behavioral observations are considered, and both presumably undisturbed and potentially disturbed periods are included. The number of sightings of calves is an approximate count because multiple counts of the same calf were possible in cases where the calf and its mother were not individually recognizable.

	1980	1981	1982
No. sightings of calves	12	16	16
No. flights	14	18	14
Calf sightings/flight	0.86	0.89	1.14
Hours in plane over whales	30.4 h	30.8 h	36.5 h
Calf sightings/hour	0.39	0.52	0.44
Calf time at surface with mother	20.4 min	17.5 min	63.1 min
Calf time at surface alone	1.6 min	12.7 min	38.2 min
Total calf time at surface	22.0 min	30.2 min	101.3 min
% of calf surface time alone	7.3%	42.1%	37.7%
Whale-hours of observation at surface	10.03 h	14.98 h	10.95 h
Calf-hours of observation/ whale-hour of observation	0.037	0.034	0.154
Calf time at surface/ sighting	1.57 min	1.89 min	6.33 min

submerged several more times toward the belly of the adult, probably nursing.

Our observations of adults and calves orienting accurately toward one another at distances up to 1.6 km apart suggest that there was acoustic communication between the two. There is possible evidence for this from the incident on 23 August 1982. The rate of low-frequency tonal frequency-modulated calls, which we suspect to be long-distance contact calls, increased while the mother and calf were swimming toward each other from some distance apart, and then ceased altogether once the two whales were joined. Several unusual higher pitched calls of undetermined origin were also recorded by a sonobuoy near the calf while the two whales were separated.

Nursing

When the lone calf of 23 August 1982 joined its mother after a separation of at least 71 min, we observed the longest probable nursing bout seen during the study. As the two animals approached each other head on, the calf dove out of sight for the first apparent nursing dive when they were still about 22 m apart. The calf dove toward the teat region of the adult six times in all, with submergences lasting 18, 11, 27, 17, 12, and 10 s (mean = 15.8 ± SD 6.37 s). These brief dives were separated by brief surfacings lasting 6, 6, 9, 11, 23, and 17 s (mean = 12.0 ± SD 6.75 s). Each surfacing included a single respiration. Nursing ended as the calf and adult dove out of sight at the same time. Although there was no apparent progression in the durations of the calf's nursing dives over the entire nursing bout, surfacings tended to lengthen, suggesting an appeasement of the calf's eagerness to nurse. The duration of the probable nursing bout from the start of the first nursing dive to the start of the deep dive by both mother and calf was 2.78 min.

The other bouts of probable nursing were shorter, sometimes < 1 min, and involved adult-calf pairs that had not recently been separated, as far as we knew. Usually, all that we could see was one or two short dives by the calf toward the teat region of the mother at the end of a surfacing sequence, followed immediately by a dive by both animals.

Other Behaviors

Aerial Activity

Bowhead whales sometimes leaped or breached from the water, forward lunged, or slapped the tail or a pectoral flipper onto the water. During breaches, 50-60% of the body length left the water. The whale emerged head first at a small angle from the vertical, usually with the ventrum down. It then twisted and fell back onto the water on its side or back. Forward lunges differed from breaches in that the body came out of the water at a shallower angle and did not twist; the whale reentered belly first. The forward lunge had a larger forward component than did the breach.

Breaches, tail slaps, and flipper slaps sometimes occurred in bouts. Within bouts, intervals between successive breaches were generally greater than those between tail or flipper slaps. For example, breaches, tail slaps, and flipper slaps by one whale that engaged in all three behaviors on 6 August 1980 were at average intervals of 46, 8, and 4 s, respectively.

The incidence of aerial activity was comparable in the 3 yr (0.60, 0.93, and 0.82 bouts/whale-hour in 1980, 1981, and 1982), but much lower than reported for spring migration. Rugh and Cubbage (1980) saw breaching by 23% of all bowheads (n = 280) observed passing Cape Lisburne, AK, in spring.

Play

Although many social interactions may involve play, we could not distinguish low levels of mating activity or aggression from play. We scored play behavior only when whales spent some time at the surface associating with an object other than a conspecific. We saw no such behavior in 1980, but several incidents in 1981 and 1982. Few such interactions have been described for other baleen whales.

LOG PLAY.—We witnessed whales playing with logs in the water on two occasions in 1981, and once in 1982. Log play, which consisted of a whale nudging, pushing, or lifting a log, lasted 5 s, 10 min, and at least 1.5 h during these three observations. In 1981, other researchers saw bowheads playing with logs twice in the same general area as our 1981 observations (C. R. Evans and J. Hickie[10]). During two of our three observations the water was ensonified by noise pulses from distant seismic exploration (Richardson et al. in press). However, there was no proof of a connection between log play and seismic noise.

Some elements of log play by bowheads were similar to play with seaweed observed in southern

[10]C. R. Evans, Biologist, and J. Hickie, Biologist, LGL Ltd., Environmental Research Associates, 22 Fisher St., King City, Ontario L0G 1K0, Canada, pers. commun. September 1981.

right whales (Payne 1972). Both involved lifting the object with the head, moving the object along the back, and patting it with the flippers. Two log-playing bowheads attempted to push the log under water with the head. This action was reminiscent of a motion commonly made by male right whales when attempting to mate with uncooperative females (Payne, pers. obs.).

CALF PLAY.–On two occasions in 1982, lone calves at the surface interacted with debris in the water, and the actions had the appearance of play.

The first incident occurred over 12.3 min on 19 August 1982, when a lone young-of-the-year calf followed a line of surface debris ~ 2 m wide, probably composed mainly of invertebrates. The calf stayed at or just below the surface and oriented directly along the windrow, changing course as the line meandered left or right. Although the calf appeared to have its mouth open slightly for brief periods, it did not appear to feed extensively, if at all. However, its movements thoroughly disrupted and dispersed the line of debris. The movements were rapid and jerky, reminiscent of any uncoordinated young mammal. The calf lunged forward while in the debris on three occasions, and slapped its tail onto the water surface twice. For ~ 30 s, it moved rapidly along the line, ventrum up, with rapid up-and-down movements of the tail for the entire time. The sequence ended when the calf dove out of sight at the end of the windrow; we did not see it with an adult. Although the incident did not seem to represent concerted feeding, this "play" by the calf may have been practice in skills required for feeding.

A second incident of "calf play" occurred on 23 August 1982. This calf was first encountered hanging quietly just below the surface, or moving forward very slowly. During slow movement, it entered an area marked by dispersed fluorescein dye from one of our dye markers (see section on Methods). The dye covered an area about 40 m by 100 m. Immediately upon entering the area of bright green water, the calf became active. During the 22.3 min of association with the dye, the calf rolled ventrum up eight times for 5-20 s each time, and moved back and forth within, and to the edge of, the dye-clear water interface. Although not as active and not beating its tail as fast as the calf in the windrow, this calf made abrupt turns of > 90° on 25 occasions during its stay in the dye, reorienting itself at the dye's edge in order to remain within the dye. The calf ultimately moved out of the dye and oriented toward an approaching adult. When the two joined, the calf apparently began nursing.

Synchrony of Activity and Orientations

There was often an impressive degree of synchrony of basic behaviors among members of quite widely spaced groups. We observed apparent synchronization of behaviors on time scales ranging from seconds to days.

Synchrony in General Activity

During 1980, we found that all or most bowheads in various areas did the same thing for up to several days. Some days later, the whales had usually moved, and whales were then found elsewhere engaged in different activities. For example, on 3 and 5 August 1980, whales north and east of Issungnak artificial island were mainly engaged in water-column feeding, with frequent defecation. By 6 and 7 August, whales in this area shifted to more surface-active behavior, interacting in groups with pushes and apparent chases. We saw little defecation at this time. On 12 August, at least 15 animals about 30-40 km west of this area were all apparently bottom feeding.

Whales were encountered in two additional areas in 1980: east of Pullen Island (19 and 20 August) and just west of McKinley Bay (19-22 August). In the Pullen Island area, all whales were mud tracking as described above. In the second area, mud also was evident, but there was much less underwater blowing. Some animals had mouths open at the surface. On 22 and 23 August 1980 almost all whales we encountered were skim feeding in groups of 10-30 animals north of McKinley Bay. However, in the Issungnak area farther west, substantial numbers of whales were still water-column feeding. On 27, 29, and 31 August 1980, whales interacted in small groups of 2-5 individuals. Some small groups oriented SSW, perhaps indicating the beginning of migration.

In summary, during 1980 (but not 1981 or 1982) we found that whales in various areas did much the same thing for up to ~ 5 d, but then shifted location, activity, or both. A partial explanation for the synchrony of behavior seen in 1980 may be that whales moved to exploit new food resources, and that the most appropriate feeding mode changed according to site-specific conditions. In the subsequent 2 yr, it appeared that whales were doing more water-column feeding in deeper water, perhaps because of a more consistent food supply.

Synchrony in Dives and Surfacings

We sometimes had the impression that all whales

in an area were synchronizing their surfacings and dives. Many were too far apart to be in visual contact. Ljungblad et al (1980) also reported synchrony among whales engaged in water-column feeding ~75 km east of Kaktovik, AK. They reported that "... whales were observed on the surface almost at regular intervals and gave the impression of resting between dives; then, suddenly, no whales would be seen in any quadrant for several minutes."

Although synchrony in surfacings by animals far apart suggests acoustic contact between animals, it is not proof of communication over that distance. The synchrony could be established through independent responses to common external cues. It could also occur if the animals were close together and visually synchronized before observations began; the observed synchrony would then be a residual phenomenon that persisted because of whales diving and surfacing for similar lengths of time. None of these possible explanations – acoustic communication, common external cues, or residual phenomenon – can be either proven or discounted at this time.

Synchrony in Orientations

Analysis of orientations provides additional evidence that widely separated whales at times synchronize their behavior during summer. Our best data were from three flights in 1980 when we flew in a straight line. At these times, we counted each individual only once. Rayleigh and χ^2 tests (Batschelet 1972) show that whale orientations were significantly nonrandom (Table 4).

For flights when we circled to make detailed behavioral observations, we analyzed orientations using the first heading noted for each surfacing of a whale. Because we were making repeated observations on the same animal in some cases, any consistency in orientations during those flights is attributable in part to different whales, and in part to subsequent surfacings of the same whale. In 1980 and 1981, the whales were oriented nonrandomly during 7 of the 11 flights with enough data for analysis (Table 4). The headings changed from day to day, however, and bore no apparent relationship to the general behavior of the whales. In 1982, no significant departures from uniformity were found during any of the five flights with sufficient data for analysis.

The headings on the latest day with observations in 1980 and 1981 usually were not in the direction to be expected at the beginning of the westward migration. On 31 August 1980, most bowheads observed while we circled north of the Tuktoyaktuk Peninsula were oriented north, east, or south (mean 121°T (true), Table 4). However, later that day on a direct flight, we found other bowheads to be oriented toward the south (mean 189°T). In this same general area, Renaud and Davis (footnote 9) also recorded a slight eastward tendency for bowheads seen on 21-24 August 1980, but a significant southwestward tendency (236°T) on 3-4 September 1980. On 8 September 1981, most whales west of Herschel Island were oriented toward the northeast (62°T), again not the direction to be expected at the beginning of westward migration. These results support our impression that most of the whales we observed were not migrating.

TABLE 4.—Bowhead orientations, judged relative to true north from the air, 1980-81. Only during the direct flights was each observation known to represent different animals. During the circling flights, each whale was scored an unknown number of times (but only once per surfacing).

Date	No. of animals with these orientations									Vector mean direction	Rayleigh test	Chi-square test P
	N	NE	E	SE	S	SW	W	NW	Total			
Direct flights												
11 Aug. 1980	16	1	3	0	5	2	10	6	43	321°	<0.001	<0.001
12 Aug. 1980	7	5	16	5	7	6	9	2	57	bimodal	n.s.	<0.025
31 Aug. 1980	1	1	1	3	8	8	0	1	23	189°	<0.001	[1]
Circling flights												
31 Aug. 1980	4	4	6	3	11	1	0	2	31	121°	<0.05	/
10 Aug. 1981	0	3	0	2	0	4	0	1	10	—	n.s.	/
10 Aug. 1981	3	1	7	2	1	6	0	1	21	bimodal	n.s.	/
13 Aug. 1981	12	9	11	1	1	0	1	1	36	43°	<<0.001	/
18 Aug. 1981	2	5	10	5	6	1	2	1	32	111°	<0.001	/
18 Aug. 1981	3	0	0	0	0	1	6	0	10	289°	<0.005	/
23 Aug. 1981	0	4	1	1	0	0	0	0	6	62°	<0.02	/
24 Aug. 1981	1	0	3	2	5	8	10	5	34	243°	<0.001	/
6 Sept. 1981	1	7	2	1	0	2	3	3	19	—	n.s.	/
7 Sept. 1981	2	5	1	1	0	2	2	3	16	—	n.s.	/
8 Sept. 1981	1	8	3	1	1	0	0	0	14	62°	<0.001	/

[1] / means cell sizes too small for a chi-square test.

We do not know whether consistent orientations represented a type of social synchrony, or whether the whales independently reacted to environmental stimuli (such as currents or wave orientations). Norris et al. (1983) and Braham et al. (1984) reported gray and bowhead whales, respectively, that may have been feeding by stationing themselves against a current. Shane (1980) has reported a similar stationing against the current for bottlenose dolphins in Texas. Gray whales in lagoons have been observed to move in the same direction as the tidal current (Norris et al. 1977), but in that case movement may have been related to avoiding shallow water as the tide receded.

Miscellaneous Observations

Speed of Travel

In 1980 and 1981, some data were gathered on bowheads visible from Herschel Island. The whales were usually > 3 km from shore, and detailed behavioral observations were infrequent. However, speed was sometimes measurable with a surveyor's theodolite. Whales rarely changed direction within any one 30 s period, so we calculated speeds from theodolite readings taken within 30 s of each other. This criterion was changed to 60 s for 30 August 1981, when a whale was followed at the surface for a long period, and changed direction relatively little.

For 1980, average speed was 5.1 km/h (n = 18, SD = 2.93) at the surface, and 4.3 km/h (n = 4, SD = 0.79) below the surface. The 1980 speeds are comparable with the most reliable estimates derived by Braham et al. (1979) and Rugh and Cubbage (1980) for migrating bowheads: 4.8-5.9 km/h and 4.7 ± SD 0.6 km/h, respectively. However, based on additional data, Braham et al. (1980) estimated the mean speed at Point Barrow in spring to be 3.1 ± SD 2.7 km/h. Speeds during active migration along the coast of Baffin Island in fall were 5.0 ± SD 1.3 km/h (n = 22) based on theodolite observations from a cliff (Koski and Davis[11]).

On 30 August 1981, an adult whale traveling east was observed continuously for 1.52 h. Its behavior was unusual—it did not submerge during the entire time. Its mean speed was 2.3 ± SD 1.26 km/h, considerably slower than the speeds mentioned above. Its mean blow interval was 10.0 ± SD 13.55 s (n = 420), significantly lower than the mean for all other undisturbed whales observed from Herschel Island (14.6 ± 9.56; n = 60; t = 2.54, $P < 0.02$).

On 8 September 1981, a mother-calf pair was observed by theodolite for 1.8 h. The average speed of the calf was 8.9 ± SD 5.57 km/h (n = 28). During this rapid movement, the calf exhibited breaches, forward lunges, tail slaps, and flipper slaps.

Associations of Bowheads with Other Species

We saw several marine mammal species in the same general areas in which we observed bowheads: ringed seals, *Phoca hispida*; white whales, *Delphinapterus leucas*; and a gray whale. There was no obvious interaction between these species and bowhead whales. The gray whale was about 500 m from the closest bowhead. The Canadian Beaufort Sea is the extreme northeastern limit of the gray whale's summer range (Rugh and Fraker 1981).

Flocks of up to 50 phalaropes (*Phalaropus* sp.) were often present near skim-feeding bowheads. These birds often alighted on water that had been disturbed by the whales, sometimes only a few meters from the whales. Phalaropes and bowheads probably feed on some of the same plankton species. The whalers used the presence of phalaropes as an indicator of where "whale feed" was present and, therefore, where whales were likely to be found (J. R. Bockstoce in press). Aside from phalaropes, we noticed glaucous gulls, *Larus hyperboreus*; arctic terns, *Sterna paradisaea*; and unidentified gulls circling briefly over whales on eight occasions.

DISCUSSION

Activities of Bowheads in Summer and Other Seasons

From 1980 through 1982 we observed a steady progression in the August distribution of bowhead whales near Tuktoyaktuk from shallow water nearshore to deeper water farther from shore (Fig. 3; Richardson et al.[12]). Such a dramatic difference in distribution over the 3 yr may be due to many different ecological and behavioral factors. Disturbance

[11]Koski, W. R., and R. A. Davis. 1980. Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Unpubl. Rep., 214 p. LGL Ltd., Toronto, for Petro-Canada Explorations, Calgary. Available from Pallister Resource Management Ltd., 700 - 6th Avenue S.W., Calgary, Alberta T2P 0T6, Canada.

[12]Richardson, W. J., R. A. Davis, C. R. Evans, and P. Norton. 1983. Distribution of bowheads and industrial activity, 1980-82. *In* W. J. Richardson (editor), Behavior, disturbance responses and distribution of bowhead whales *Balaena mysticetus* in the eastern Beaufort Sea, 1982. Unpubl. Rep., p. 269-357. LGL Ecological Research Associates, Inc., Bryan, TX, for U.S. Minerals Management Service, Reston, VA. Available from Minerals Management Service Alaska OCS Region, P.O. Box 101159, Anchorage, AK 99510.

by industrial activity in nearshore waters is also a possibility (see footnote 12). The fact that predominant feeding modes shifted from year to year is consistent with the "variable food supply" explanation. In 1980, whales in shallow water exhibited bottom feeding and skim feeding, while whales in slightly deeper water apparently fed in the water column. In 1981, most feeding appeared to be water-column feeding and skim feeding. In 1982, whales made long dives and presumably were often feeding in the water column.

Bowhead whales have finely fringed baleen, the longest of any whale species, and are adapted to strain small zooplankters from the sea. Stomach contents indicate that, at least in Alaskan waters, bowheads feed mainly on copepods, euphausiids, and amphipods (Marquette et al. 1982). Summering bowheads tend to occur at locations where copepod abundance is above average (Griffiths and Buchanan footnote 7). Lowry and Burns (1980) examined five whales killed off Barter Island, AK, in autumn and found about 60% copepods and about 37% euphausiids in their stomachs. However, all five whales may have fed at least partially near the sea floor; about 3% of the stomach contents consisted of mysids, amphipods, other invertebrates, and fish. Durham (1972) also suggested, based on stomach content analyses showing mud-dwelling tunicates, vegetation, silt, and small pebbles, that bowheads feed at times near the bottom. Lowry and Burns concluded from stomach content analyses that "...a feeding dive probably involves swimming obliquely from surface to bottom and back, feeding the entire time." Although this may be true at times, there is no direct information on underwater feeding behavior. We suspect that bowheads can detect concentrations of prey and open their mouths when appropriate. The bowhead whale is perhaps a more catholic feeder than once thought, capable of taking advantage of many different types of prey items at various positions in the water column and near the bottom. Year-to-year changes in distributions and availability of prey may account for the distributional changes that we have observed, but data on yearly changes in prey are lacking.

During spring migration around Alaska, bowhead whales appear to do little feeding; their stomachs usually are nearly empty (Marquette et al. 1982). On the other hand, feeding continues in autumn after bowheads have moved from the Canadian to the eastern part of the Alaskan Beaufort Sea (Lowry and Burns 1980; Marquette et al. 1982). Some feeding occurs in autumn as far west as the Point Barrow area (Lowry et al. 1978; Braham et al. 1984), and perhaps farther west off the Soviet coast (Johnson et al. 1981).

Feeding is not the only activity of bowheads in summer. Socializing, perhaps with occasional sexual activity, is also important. In 1982, however, there was less socializing than in 1980-81. Whales were in close proximity to each other less in 1982. This year-to-year difference in proximity may be related to the difference in type of feeding. While skim feeding at the surface, whales are often in close echelons. The proximity necessary for echelon feeding offers more chance for socializing, and socializing before or after feeding in echelon may be important to that mode of feeding. When whales appear to feed in the water column, however, they usually do not stay as close together. Thus, this type of feeding may neither require nor stimulate aggregations of animals, and the suspected predominance of water-column feeding in 1982 may explain the low socializing rate that year. Even when there is no close socializing, however, animals are often in a dispersed group within which acoustic communication is probably possible. Our observations of surfacing and dive synchrony by whales spread over distances of several kilometers indicate that they may have been in touch by acoustic communication.

The primary mating period of bowhead whales occurs in spring, including the spring migration (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Johnson et al. 1981; Nerini et al. 1984). We saw some evidence for sexual activity in the Canadian Beaufort Sea in both 1980 and 1981, but not in 1982. Even the active rolling at the surface that we observed in 1981, however, was not as boisterous as observed by Everitt and Krogman in spring. Also, we found an indication of less social activity in late August-early September than in early August. This apparent waning in social activity may be a continuation of the waning of sexual activity that started in late spring.

Many calves are born in winter or spring before the whales reach Point Barrow, although some may be born in early summer (Davis et al. footnote 9). During summer, the activities of female bowheads with accompaning calves are closely coordinated with those of their calves, and differ in some details from the activities of other adult bowheads (this study; Würsig et al. 1984). At least some calves remain with their mothers for the fall migration (Davis and Koski 1980). We know of no information concerning the age of weaning of bowhead calves, but in the closely related right whale, at least some calves remain with their mothers for 1 yr and ultimately separate from their mothers after returning to the

wintering area (Taber and Thomas 1982).

Aerial activity similar to what we observed in the eastern Beaufort Sea–breaches, tail slaps, pectoral flipper slaps, and rolls–has been observed in bowheads during spring migration (Rugh and Cubbage 1980; Carroll and Smithhisler 1980). It appears that aerial behavior is more frequent during spring migration than on the summer feeding grounds, and this may be related to the high levels of social-sexual activities during spring.

Comparisons with Other Baleen Whales

Bowhead whales spend their entire lives in arctic and near-arctic waters. This habit separates them from all other baleen whales, which may move into temperate or subtropical waters (Lockyer and Brown 1981). However, behavior is in large part determined by feeding mode and related ecological factors (Gould 1982), and here similarities between bowhead whales and several other species are evident.

Gray, bowhead, and right whales are often found in shallow water, and all three species feed on small invertebrates. Gray whales usually feed near the bottom (Bogoslovskaya et al. 1981; Nerini and Oliver 1983), whereas right and bowhead whales may skim their food at or near the surface (see Watkins and Schevill 1976, 1979 for right whales). But all three species are adaptable in feeding behavior. Gray whales apparently will feed on mysids associated with kelp (Darling 1977) or on crab *Pleuroncodes* in the water column (Norris et al. 1983). Right whales also feed below the surface, probably straining swarms of copepods and other small invertebrates in the water column (Pivorunas 1979). While it has long been known that bowhead whales feed at the surface and in the water column (Scoresby 1820), it was recently established from stomach content analyses (Durham 1972; Lowry and Burns 1980), and by observing bowhead whales surfacing with muddy water streaming from their mouths (this study), that bowheads sometimes feed near or on the bottom. It is not surprising that there are many similarities in the behavior of these species. Bowhead and right whales, in particular, are morphologically and taxonomically quite similar, and appear to obtain their food in very much the same ways. In fact, Rice (1977), mainly relying on a detailed comparison of morphology of bowhead and right whales, suggested that they be put in the same genus, *Balaena*.

The sleeker rorquals (Balaenopterid whales) generally gather their food more actively by lunging through concentrations of prey, and at least in the case of humpback whales, have developed complicated behavioral strategies for confining and concentrating their prey (Jurasz and Jurasz 1979; Hain et al. 1982). The rorquals are more often found in deeper water far from shore, and their behavior in general appears to be less similar to that of the bowhead whale than its behavior is to that of gray and right whales.

Gray whales spend part of the winter in warm water, near the shores of Baja California, and most of the summer they feed in the northern Bering and southern Chukchi Seas. Western Arctic bowheads make much shorter migrations, spending their winter in the pack ice of the Bering Sea and their summer predominantly in the Beaufort Sea. The two species thus use the Bering Sea at different seasons and for different purposes–gray whales to feed in summer and bowheads apparently to mate and calve in winter. Like bowhead whales summering in the Beaufort Sea, the primary activity of gray whales summering in the Bering and Chukchi Seas is feeding. However, both bowheads and gray whales (Sauer 1963; Fay 1963) occasionally socialize during summer.

Right whales, like bowhead whales, often appear to feed in the water column or at the surface (Watkins and Schevill 1976, 1979) and may stay in the same general area for days. While skim feeding, both species at times aggregate into echelons. In right whales, these echelons usually consist of only 3-6 whales (Payne, pers. obs.), while up to 14 bowhead whales have been seen skim feeding in echelon. However, Payne observed right whales during winter when little feeding occurs, so apparent differences in feeding details may be due to seasonal factors.

Apparent differences between the social activity of bowheads and right whales may also be largely attributable to the different times of year when they have been studied. The same kinds of nudges and pushes have been observed for interacting whales of both species, but the winter-spring social activity of right whales is much more boisterous than the summer social activity of bowheads. Observations of bowhead whales in spring indicate that their social-sexual activity at that season can be as boisterous as is seen in mating groups of right whales (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Rugh and Cubbage 1980; Johnson et al. 1981). The belly-up position of a female bowhead photographed in spring in the Alaskan Beaufort Sea (Everitt and Krogman 1979) indicates that females may attempt to evade potential mates who pursue them in large mating aggregations in the same way that female right

whales evade males in Argentine waters (Payne and Dorsey 1983). A photograph showing a remarkably similar mating group of right whales is shown in the article by Payne (1976). The fact that similar-looking social aggregations are seen in both species argues for a similar social system, although it does not show that the social systems are similar in all details.

Female right whales have young only at intervals of 3 yr or more (Payne, pers. obs.). The same appears to be true of bowheads (Davis et al. footnote 9; Nerini et al. 1984). This long calving interval may help to explain why bowhead and right whales have not made as dramatic a recovery from commercial exploitation as has, for example, the gray whale. Payne also found that right whale females that calve along the shore of southern Argentina in winter are usually not present in the years between calving. Each winter, a different segment of the population of mature females is present, in a 3-yr cycle. It is not known whether this cycling extends to the summer feeding grounds of these right whales. During the present 3-yr study, year-to-year variation in feeding and social behavior was dramatic, but we do not know whether this was due in part to some cyclic and synchronized activity of individual whales. We suspect that variable prey distibution was largely responsible.

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FOOD HABITS OF BAIT-CAUGHT SKIPJACK TUNA, *KATSUWONUS PELAMIS*, FROM THE SOUTHWESTERN ATLANTIC OCEAN

LISA ANKENBRANDT[1]

ABSTRACT

Stomach contents of skipjack tuna captured in 1981-82 by live pole-and-line vessels off the southern coast of Brazil were analyzed for the presence of larval and juvenile skipjack tuna. The percentage frequency of occurrence, percent number, and percent volume were evaluated. Of the 1,041 stomachs that were examined for food, 436 were empty. The mean volume of food in all stomachs analyzed was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey.

The gonostomatid *Maurolicus muelleri* and the euphausiid *Euphausia similis* were the principal foods. Other important foods were the chub mackerel, *Scomber japonicus*; the frigate tuna, *Auxis thazard*; gempylids; trichiurids; and carangids. In the study area, adult skipjack tuna were not found to feed on their young.

Kruskall-Wallis nonparametric one-way analysis of variance was used to test for differences in the mean volumetric ratios of food items in relation to skipjack size. The percentage of *E. similis* in the diet was found to decrease, while the proportion of *M. muelleri* was found to increase with increasing skipjack size. Seasonal variations in the diet were also examined and discussed.

Apparently the anatomy of their gill raker apparatus allows skipjack to ingest a wide variety of prey types above a minimum size. These variations in the food can be attributed to the number and size of the prey species in an area.

A Brazilian skipjack pole-and-line fishery has been developing in the Rio de Janeiro area since 1979 (Fig. 1). Because skipjack tuna, *Katswonus pelamis*, is one of the major tuna species harvested at maximum sustainable yield in the tropical and subtropical oceans (Kearny 1976; Evans et al. 1981), estimation of the fishery potential requires information on the distribution and concentration of its spawning stock. One technique used to determine the existence of a spawning stock is to quantify the distribution of its larvae. Obviously, the presence of large numbers of larvae would indicate a spawning stock occupies an area.

Knowledge of the distribution and abundance of juvenile skipjack tuna is limited. Occasionally, specimens have been found in experimental plankton hauls or in the stomachs of apex predators (Kearny 1976). From ichthyoplankton surveys, Matsuura (1982) and Nishikawa et al. (1978) reported larvae in warm tropical waters north of the study area (Fig. 1), and juvenile skipjack tuna have been found in the stomachs of adult skipjack tuna captured off west Africa and in the Caribbean (Suarez-Caabro and Duarte-Bello 1961; Klawe 1961; Dragovich 1970; Dragovich and Potthoff 1972). Their occurrence in the diet of central and south Pacific skipjack tuna caught by pole-and-line has been used to deduce their distribution and abundance (Waldron and King 1963; Nakamura 1965; Argue et al. 1983).

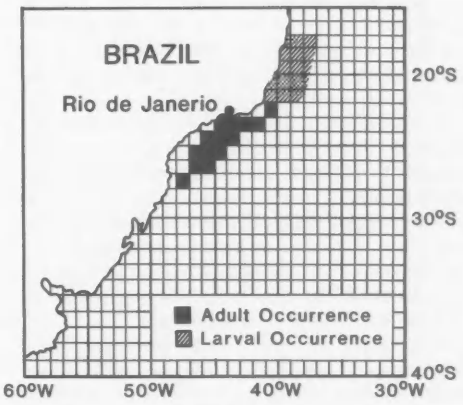

FIGURE 1.—Solid area indicates fishing localities from where skipjack tuna stomachs were obtained. Hatched area shows larval occurrence (Matsuura 1982).

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038; present address: School of Fisheries, University of Washington, Seattle, WA 98195.

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Dragovich (1969) reviewed existing information on the food habits of Atlantic skipjack tuna. Since that time food habits have also been reported in studies by Dragovich (1970) and Dragovich and Potthoff (1972) for skipjack from the East and West Atlantic and by Batts (1972) for skipjack in North Carolina waters. Zavala-Camin (1981) examined predator-prey interactions of fishes, including skipjack captured north of the area in this study.

The primary objective of this study was to discover if skipjack tuna feed upon their young. The presence of juveniles in bait-caught skipjack stomachs would verify the study area as a spawning-rearing ground. Knowledge of the prey and their relative importance also contributes to the understanding of prey-predator interactions, which affect population distributions and fluctuations.

MATERIALS AND METHODS

Stomach samples for this study were collected on a monthly basis from October 1981 to December 1982 from skipjack tuna caught off Rio de Janeiro (Fig. 1). National Marine Fisheries Service (NMFS) personnel collected stomachs from frozen fish transhipped to Puerto Rico, and Superintendencia do Desenvolviemento da Pesca (SUPEDE) personnel sampled fish landed locally in Rio de Janeiro. Fish from the Puerto Rican source were caught within 1 mo prior to sampling; fish from the Brazilian source were sampled 3 to 5 d after the recorded catch date. The sampling design required collecting about 15 stomachs from each 10 cm length group, measured to the nearest cm per month. However, the number of stomachs collected was dependent on the catch-size distribution. Once the stomach was removed from the fish, it was preserved in 10% buffered Formalin[2] and shipped to the Southwest Fisheries Center (SWFC) for analysis.

Stomachs were examined from 1,041 fish between 44 and 81 cm fork length. In the laboratory each stomach was opened. The volume of the food bolus was measured, and the contents were identified to the lowest possible taxon. The taxonomic groupings were then measured by volumetric displacement, and the individuals counted. Whole undigested fish were identified by comparing external characters with those described in published keys or with identified museum specimens from Scripps Institution of Oceanography, La Jolla, CA. Digested animals, particularly juvenile scombrids, were identified by vertebral, gill raker, and fin ray counts, as well as other skeletal characteristics, described by Potthoff and Richards (1970), Miller and Jorgenson (1973), and other published keys. Cephalopods were identified by comparing beak characters with published illustrations, descriptions, and keys (see Wolff 1981). Crustaceans and other invertebrates were identified by specialists from Scripps Institution of Oceanography and SWFC.

The occurrence of bait in the stomachs may have biased the relative importance of fish in the diet. The bait primarily consisted of *Sardinella brasiliensis*, *Harengula jaguana*, and *Engraulis anchoita*; however, other fish families may have been included in the captured bait. The sardines were readily identifiable from their external characters and usually were undigested. The anchovies, in contrast, were often quite digested, creating difficulties in identification. Gary Nelson[3] nevertheless was able to verify these fish as *Engraulis anchoita*. Although the least digested item in the stomach was usually the last meal (bait), stomachs were removed from a few days to 1 mo after capture, and presumably postmortem digestion occurred. As a result, the degree of digestion was not a reliable indication of distinguishing bait from natural prey. The time required for complete gastric evacuation of smelt fed to skipjack tuna is estimated to be 12 h (Magnuson 1969). Although the bait was captured in nets from bays and estuaries (Rinaldo[4]), Matsuura et al. (1978, 1981) have confirmed that a spawning stock of *E. anchoita* does exist in waters inhabited by skipjack tuna. It is unlikely that the sardines served as prey for skipjack. However, I could not distinguish between *E. anchoita* consumed as natural food and as bait. Therefore, although these species were considered bait, some may have been ingested as natural food. Bait was not considered prey, and stomachs containing only these species were treated as empty.

Two methods of analysis were employed to rank the food items in terms of availability and importance to the skipjack tuna:

1) An index of relative importance (*IRI*) was calculated for each prey type in terms of numbers, volumes, and frequencies (Pinkas et al. 1971):

$$IRI = (N + V)F$$

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]G. J. Nelson, Department of Ichthyology, American Museum of Natural History, New York, NY 10024, pers. commun., May 1982.

[4]R. R. Rinaldo, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., June 1982.

where N = numerical percentage
V = volumetric percentage
F = frequency of occurrence percentage.

2) The mean volumetric ratio measurement (*MVRM*) was used to illustrate the biomass importance of prey items without the numeric exaggeration implicit in the *IRI* (John Hedgepeth[5]). The *MVRM* was calculated from the volumetric analysis of individual stomachs with each prey item contributing to the total stomach volume. *MVRM* for each food type is expressed as

$$MVRM = \bar{r}_j \times 100 = \text{mean volumetric percentage of prey } j \text{ to the total volume of } n \text{ stomachs}$$

where N = number of stomachs in a given strata
V_{ij} = volume of prey type j in stomach i

$$V_i = \sum_{j=1}^{6} V_{ij} = \text{total volume of stomach } i$$

$$r_{ij} = \frac{V_{ij}}{V_i} = \text{ratio of prey } j \text{ to the total volume of stomach } i$$

$$\bar{r}_j = \frac{\sum_{i=1}^{n} r_{ij}}{n} = \text{mean volumetric ratio of prey } j \text{ to the total volume of } n \text{ stomachs.}$$

Both the *IRI* and the *MVRM*, which examine different aspects of the diet, were used to evaluate seasonal variations in skipjack tuna food habits. The *IRI* presents a biased estimate caused by the numerical percentage; the relative importance of small numerous organisms, like euphausiids, is exaggerated in the *IRI* because of their high numbers, when actually they may represent the same food value as a few large fish. The *MVRM* is an expression of frequency of occurrence and volume without a numeric bias, but does not provide any information on prey abundance. The *IRI* contains information on the availability of the prey in the environment in terms of numbers, while the *MVRM* provides an indication of its energetic importance to the fish.

The *MVRM*s were stratified by fish length and annual quarter (Fig. 2), and tested with the Kruskal-Wallis nonparametric one-way analysis of variance to evaluate differences in diet with changes in size.

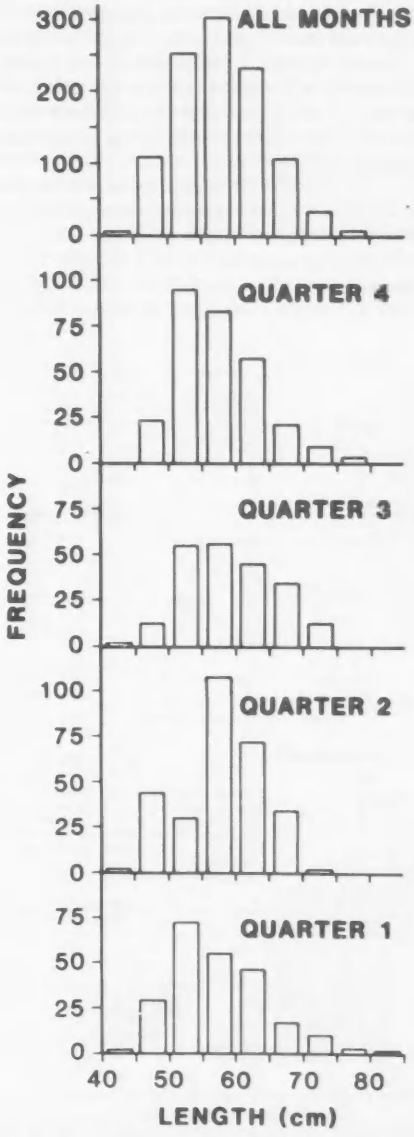


FIGURE 2.—Length-frequency distribution of skipjack tuna from which stomachs were collected.

[5]J. B. Hedgepeth, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun., April 1982.

RESULTS

Food Composition

Of the 1,041 stomachs that were examined, 436 were empty. The mean volume of food in all stomachs examined was 36.9 mL, of which 18.9 mL was bait and 18.0 mL was prey. A complete list of the stomach contents in terms of numbers, volume, and frequency is presented in Appendix Table 1. No larval or juvenile skipjack were found in the stomach contents. Overall contributions of each category are presented in Figure 3.

In terms of the *MVRM*, the gonostomatid *Maurolicus muelleri* was the major prey item (*MVRM* = 26.7%). The euphausiid *Euphausia similis*, with the highest *IRI*, was also important (*IRI* = 1,998). These items were major constituents of the diet throughout the year. Other important fishes in terms of both the

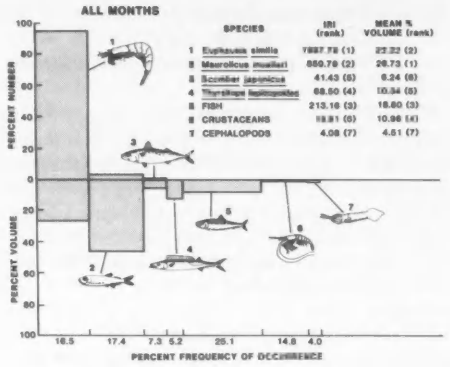
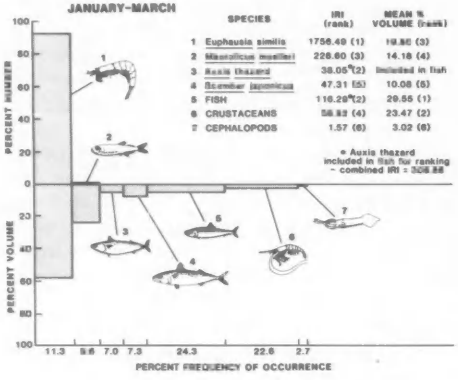
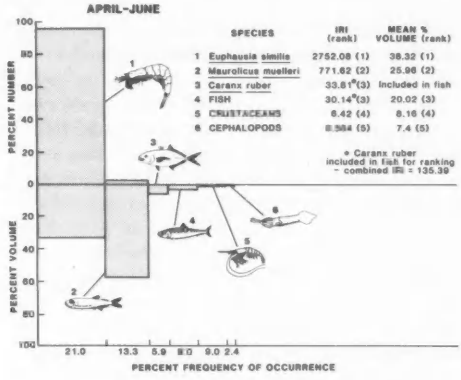
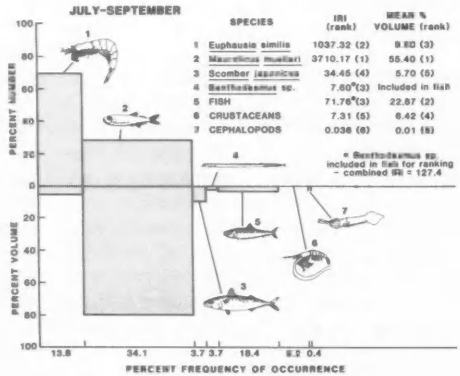

ALL MONTHS
SPECIES
IRI (rank)
MEAN % VOLUME (rank)
1 Euphausia similis 7937.78 (1) 22.22 (2)
2 Maurolicus muelleri 850.76 (2) 26.73 (1)
3 Scomber japonicus 41.43 (8) 6.24 (8)
4 Thyrsitops lepidopoides 68.50 (4) 10.34 (3)
5 FISH 213.16 (3) 18.60 (3)
6 CRUSTACEANS 19.81 (6) 10.96 (4)
7 CEPHALOPODS 4.08 (7) 4.61 (7)
PERCENT NUMBER
PERCENT VOLUME
16.5 17.4 7.3 5.2 25.1 14.8 4.0
PERCENT FREQUENCY OF OCCURRENCE

FIGURE 3.–Index of relative importance (IRI) plots for selected food items of skipjack tuna caught during 1982. The food categories are ranked in terms of IRI and MVRM.


JANUARY–MARCH
SPECIES
IRI (rank)
MEAN % VOLUME (rank)
1 Euphausia similis 1756.49 (1) 19.86 (3)
2 Maurolicus muelleri 226.60 (3) 14.18 (4)
3 Auxis thazard 38.05*(2) Included in fish
4 Scomber japonicus 47.31 (5) 10.08 (5)
5 FISH 116.28*(2) 29.55 (1)
6 CRUSTACEANS 58.83 (4) 23.47 (2)
7 CEPHALOPODS 1.57 (6) 3.02 (6)
* Auxis thazard included in fish for ranking – combined IRI = 306.88
PERCENT NUMBER
PERCENT VOLUME
11.3 9.6 7.0 7.3 24.3 22.6 2.7
PERCENT FREQUENCY OF OCCURRENCE


APRIL–JUNE
SPECIES
IRI (rank)
MEAN % VOLUME (rank)
1 Euphausia similis 2752.08 (1) 38.32 (1)
2 Maurolicus muelleri 771.62 (2) 25.96 (2)
3 Caranx ruber 33.61*(3) Included in fish
4 FISH 30.14*(3) 20.02 (3)
5 CRUSTACEANS 6.42 (4) 8.16 (4)
6 CEPHALOPODS 0.564 (5) 7.4 (5)
* Caranx ruber included in fish for ranking – combined IRI = 135.39
PERCENT NUMBER
PERCENT VOLUME
21.0 13.3 5.9 9.0 9.0 2.4
PERCENT FREQUENCY OF OCCURRENCE


JULY–SEPTEMBER
SPECIES
IRI (rank)
MEAN % VOLUME (rank)
1 Euphausia similis 1037.32 (2) 9.80 (3)
2 Maurolicus muelleri 3710.17 (1) 55.40 (1)
3 Scomber japonicus 34.45 (4) 5.70 (5)
4 Benthodesmus sp. 7.60*(3) Included in fish
5 FISH 71.76*(3) 22.87 (2)
6 CRUSTACEANS 7.31 (5) 6.42 (4)
7 CEPHALOPODS 0.036 (6) 0.01 (6)
* Benthodesmus sp. included in fish for ranking – combined IRI = 127.4
PERCENT NUMBER
PERCENT VOLUME
13.9 34.1 3.7 3.7 18.4 8.2 0.4
PERCENT FREQUENCY OF OCCURRENCE

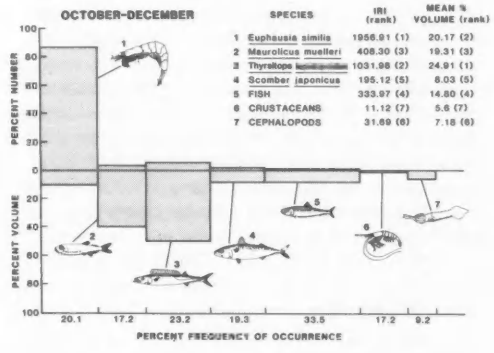

OCTOBER–DECEMBER
SPECIES
IRI (rank)
MEAN % VOLUME (rank)
1 Euphausia similis 1956.91 (1) 20.17 (2)
2 Maurolicus muelleri 408.30 (3) 19.31 (3)
3 Thyrsitops lepidopoides 1031.98 (2) 24.91 (1)
4 Scomber japonicus 195.12 (5) 8.03 (5)
5 FISH 333.97 (4) 14.80 (4)
6 CRUSTACEANS 11.12 (7) 5.6 (7)
7 CEPHALOPODS 31.69 (6) 7.18 (6)
PERCENT NUMBER
PERCENT VOLUME
20.1 17.2 23.2 19.3 33.5 17.2 9.2
PERCENT FREQUENCY OF OCCURRENCE

FIGURE 4.–Index of relative importance (IRI) plots for selected food items of skipjack tuna. The complete data are divided into four 3-mo quarters (I-IV). The food categories are ranked in terms of IRI and mean percent volume.

IRI and *MVRM* were chub mackerel, *Scomber japonicus*, and *Thyrsitops lepidopoides*[6] (Fig. 3). Crustaceans other than *E. similis* occurred frequently in the stomachs (F = 22.6%), but as a relatively low percentage of the total volume (V = 2.0%). Cephalopods were usually insignificant in the diet (see below). Pteropods, siphonophores, beetles, rocks, and unidentified materials were the constituents of the miscellaneous category (App. Table 1).

Seasonal Variations

The data were divided into four quarters: January-March 1982 (I), April-June 1982 (II), July-September 1982 (III), October-December 1981 and 1982 (IV). The results (App. Tables 2-6) are illustrated in Figures 4 and 5 both with the *IRI* and the *MVRM* of dominant food items in each quarter. Note that items important in one quarter may be negligible or absent in another. When evaluated in terms of *MVRM*, the prey ranks sometimes did not coincide with those determined by the *IRI* (Figs. 4, 5). Based on the *IRI*, *E. similis* was the dominant food in the first quarter, followed by other fish and *M. muelleri* (Fig. 4). According to the *MVRM*, other fishes, other crustaceans, and *E. similis* were ranked first, second, and third in importance, respectively. The importance of *E. similis* in this quarter based on the *IRI* was exaggerated by their high frequencies of occurrence. *Scomber japonicus* and frigate tuna, *Auxis thazard*, were secondary in importance to *M. muelleri* as the main fish species consumed.

The rankings of the food categories in the second quarter were the same for both the *IRI* and the *MVRM* (Fig. 4). *Euphausia similis* and *M. muelleri* were the dominant food items, followed by *Caranx ruber*.

[6]Identified by Y. Matsuura, Universidade de São Paulo, Instituto Oceanografico, São Paulo, Brazil, October 1984.

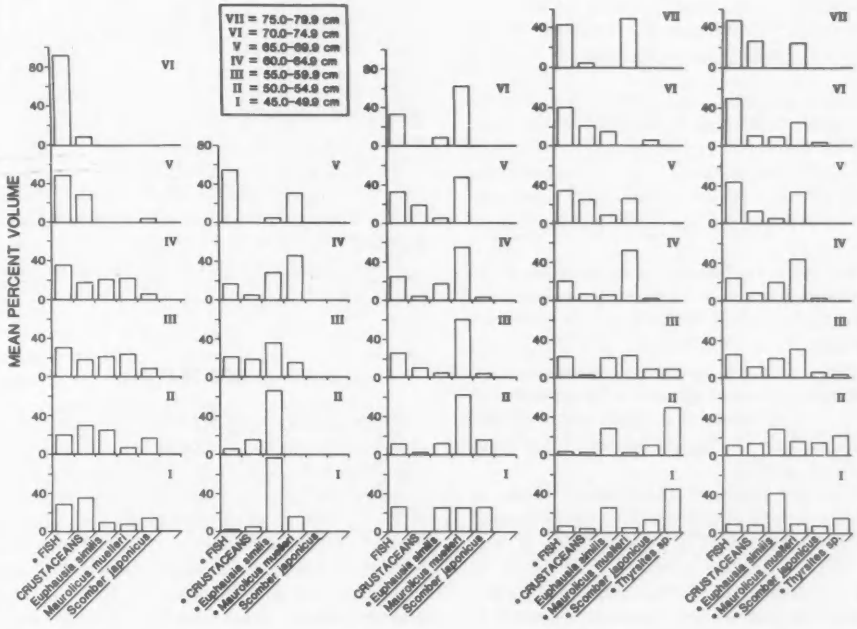


FIGURE 5.– Relative importance based on mean volumetric ratio of selected food items for skipjack tuna grouped by length for each quarter (I-IV) and all months. * indicates a significant difference ($P < 0.05$) in the mean percent volume of that food item by length when tested with the Kruskal-Wallis nonparametric one-way analysis of variance.

The principal food item in the third quarter based on both measurements was *M. muelleri* (Fig. 4). The ranks for the other items did not correspond. *Euphausia similis* was second in importance according to the *IRI*, but ranked third next to other fish based on the *MVRM*. *Scomber japonicus* and *Benthodesmus* sp. were the predominant species consumed in the fish category.

The *IRI* and *MVRM* ranks in the fourth quarter corresponded with the exception of the principal prey type (Fig. 4). Again, *E. similis* ranked first according to the *IRI*, but *Thyrsitops lepidopoides* was the primary food item based on the *MVRM*. Cephalopods, mainly *Argonauta* sp., were consumed in significant proportions in this quarter (*IRI* = 31.7, *MVRM* = 7.2%).

In summary, *M. muelleri* and *E. similis* predominated in the skipjack tuna diet during all quarters (Fig. 3). With the exception of the second quarter, *S. japonicus* was an important food item. *Benthodesmus* sp., *C. ruber*, *A. thazard*, as well as the cephalopod, *Argonauta* sp., also proved important in specific quarters. The importance of *T. lepidopoides* in Figure 3 was exaggerated by its predominance in the fourth quarter.

Variations with Size

As might be expected, basic dietary changes occur as the skipjack tuna grow. Nakamura (1965), Alverson (1963), Batts (1972), Dragovich and Potthoff (1972), and Wilson (1982) observed a decrease in the relative importance of crustaceans and an increasing importance of fish in the diet, as the skipjack size increased.

To evaluate the relationship between size and food habits, the skipjack were arbitrarily divided into seven 5 cm groups (Fig. 2). For each prey category the *MVRM*s were stratified by size group and quarter (App. Tables 6-10, Fig. 5). Trends reported in the results for length groups > 70 cm may not represent feeding habits of skipjack tuna from the study area because the sample sizes were too small (Fig. 2, App. Table 6).

There were no significant differences ($P < 0.05$) in diet and size in the first quarter except in the amount of other fish consumed (Fig. 5, App. Table 7). The *MVRM* of this category increased from 28.7% in skipjack 45.0-49.9 cm to 91.7% in fish 75.0-79.9 cm.

In the second quarter the proportions of other fish, other crustaceans, *E. similis*, and *M. muelleri* significantly changed with size (Fig. 5, App. Table 8). The larger skipjack tuna ate more fish (*MVRM* = 1.7% in the 45.0-49.9 cm size class to *MVRM* = 54.1% in the 75.0-79.9 cm size class) and more *M. muelleri* (*MVRM* = 15.4% to *MVRM* = 30.3%) than the smaller skipjack. As their size increased, skipjack decreased their consumption of *E. similis* from MVRM = 76.9% to *MVRM* = 4.5%. There was a significant difference between size classes ($P < 0.05$) in the *MVRM* of other crustaceans in the diet, but this difference seemed uncorrelated to increases in size.

In the third quarter there were no significant differences in the diet with increasing size except that the *MVRM* of *E. similis* decreased from 25.0% to 8.0% (Fig. 5, App. Table 9).

Thyrsitops lepidopoides was eaten by the smaller skipjack (45-59.9 cm) only in the fourth quarter (Fig. 5, App. Table 10). Although there were significant differences ($P < 0.05$) in the diets between the seven size groups during this period, these differences again seemed unrelated to increasing size.

In summary, when the data on *T. lepidopoides* were included with the rest of the fish data, there were no significant differences between size groups in the proportions of other fish consumed throughout the year (Fig. 5, App. Table 6). The *MVRM* of *E. similis* in the diet decreased from 42.5% in skipjack tuna 45.0-49.9 cm to 0.0% in skipjack 75.0-79.9 cm. There were significant differences in the percentages of *M. muelleri* and *S. japonicus* between the size classes. There were no significant differences in the *MVRM* of other crustaceans with changes in size.

As reported in the studies of the food habits of skipjack tuna referred to above, the stomach contents of skipjack from this area indicated the basic dietary changes associated with increasing size: a significant decrease in the proportion of *E. similis*, the predominant crustacean prey, and an increase in proportion of *M. muelleri*, the predominant fish prey.

DISCUSSION

Several studies have reported that skipjack tuna feed predominantly on euphausiids and gonostomatids. Dragovich and Potthoff (1972) reported that the gonostomatid *Vinciguerria nimbaria* contributed 44.7% by volume to the diet of skipjack tuna from the Gulf of Guinea. Zavala-Camin (1981) reported *M. muelleri* and euphausiids as dominant food items in 36 stomachs of skipjack caught off Brazil. Alverson (1963) reported skipjack tuna captured in the eastern tropical Pacific fed primarily on euphausiids (47% by volume, in 37% of the stomachs), followed in importance by the gonostomatid *Vinciguerria lucetia* (10% by volume). The abundance of euphausiids in

the stomachs of skipjack, compared with larger scombrids, may be a result of smaller gill raker gaps in skipjack (Magnuson and Heitz 1971).

The importance of other fishes as food for western Atlantic skipjack tuna observed in this study has been previously reported. Dragovich (1970) found a predominance of fish in the stomachs of skipjack caught off the eastern United States and the Caribbean. Suarez-Caabro and Duarte-Bello (1961) found that fishes constituted 75% of the total volume, followed by squid (23%) and crustaceans (2%), in the stomachs of Cuban skipjack. Zavala-Camin (1981) observed that fish constituted 38.9%, crustaceans 22.2%, and mollusks 2.8% of the total stomach volume of Brazilian skipjack.

CONCLUSIONS

The multiplicity of prey found in this as well as other studies indicates that tunas are perhaps nonselective feeders, and stomach contents are probably determined by prey availability (Hotta and Ogawa 1955; Alverson 1963; Batts 1972; Perrin et al. 1973; Argue et al. 1983). Therefore, if the larval and juvenile skipjack were available in significant numbers, then one would expect them to occur in the diet of the adults.

Their absence in the diet was caused by two possible results. First, the young remained among the unidentified portion of the stomach contents; however, skipjack tuna have distinctive vertebral characteristics which were probably not discounted in the analysis (Potthoff and Richards 1970). Second, the adults did not spawn in the study area. Young skipjack should be found in the stomach contents of spawning adults (Argue et al. 1983). Goldberg and Au[7] found no evidence of spawning in skipjack collected from the Brazilian fishery. These results are consistent with the absence of larval and juvenile skipjack in the diet of the adults in this study.

The southernmost distribution boundary for larval skipjack tuna is the 24°C surface isotherm (Argue et al. 1983). Matsuura (1982) found no larval skipjack in ichthyoplankton surveys south of lat. 21°S in this area, where temperatures range from 21° to 24°C (Evans et al. 1981).

These results are consonant with those of Argue et al. (1983); juvenile skipjack tuna were absent from samples of adult stomachs taken in subtropical south Pacific waters. The adult skipjack in this investigation did not feed on their young. The absence of cannabilism suggests that larvae and juveniles were not significantly abundant to serve as forage of the adults, and therefore probably do not occur in this cooler southern water.

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Gareth Nelson, Richard Rosenblatt, Kurt Schaeffer, and Betsy Stevens assisted in the identification of the fishes. The euphasiid was identified by Edward Brinton. Robert Olson assisted in the identification of cephalopod beaks. Angeles Alvarino assisted in the identification of other invertebrates.

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APPENDIX

APPENDIX TABLE 1.—List of prey items and other ingested materials found in the stomachs of 1,041 skipjack tuna caught off southern Brazil, from October 1981 to December 1982.

	Numbers		Volume		Occurrence	
Prey items	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	12.0	0.003	4.5	0.024	6.0	0.576
Mysidacea						
Eucopiidae	220.0	0.057	42.4	0.226	22.0	2.113
Lophogastridae	24.0	0.006	1.7	0.009	3.0	0.288
Isopoda	1.0	0.000	0.1	0.001	1.0	0.096
Flabellifera	7.0	0.002	2.1	0.011	7.0	0.672
Amphipoda	22.0	0.006	1.5	0.008	2.0	0.192
Gammaridea	16.0	0.004	5.1	0.027	10.0	0.961
Euphausiidae	139.0	0.036	3.9	0.021	15.0	1.441
Euphausia sp.	50.0	0.013	0.6	0.003	1.0	0.096
Euphausia similis	368,632.0	94.785	4,895.3	26.122	172.0	16.523
Stylocheiron sp.	1.0	0.000	0.3	0.002	1.0	0.096
Caridea	3.0	0.001	2.3	0.012	3.0	0.288
Macrura						
Scyllaridae	1.0	0.000	0.2	0.001	1.0	0.096
Unid. Phyllosoma larvae	1.0	0.000	0.1	0.001	1.0	0.096

APPENDIX TABLE 1.—*Continued.*

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Brachyura	5.0	0.001	0.7	0.004	1.0	0.096
Portunidae	1.0	0.000	0.1	0.001	1.0	0.096
Unid. megalops	102.0	0.026	32.0	0.171	27.0	2.594
Unid. zooea	555.0	0.143	30.2	0.161	24.0	2.305
Unid. Decapoda	7.0	0.002	0.6	0.003	2.0	0.192
Unid. Crustacea	96.0	0.025	11.0	0.059	26.0	2.498
Mollusca						
Gastropoda	1.0	0.000	0.1	0.001	1.0	0.096
Cavolina sp.	101.0	0.026	6.0	0.032	7.0	0.672
Cephalopoda						
Teuthoidea	4.0	0.001	26.0	0.139	4.0	0.384
Thysanoteuthidae	2.0	0.001	10.0	0.053	1.0	0.096
Ommastrephidae	35.0	0.009	55.1	0.294	18.0	1.729
Loliginidae	2.0	0.001	10.5	0.056	2.0	0.192
Histioteuthidae	1.0	0.000	1.0	0.005	1.0	0.096
Onychoteuthidae	13.0	0.003	6.0	0.032	2.0	0.192
Octopoda						
Argonautidae						
Argonauta sp.	20.0	0.005	75.9	0.405	11.0	1.057
Unid. Cephalopoda	4.0	0.001	1.3	0.007	3.0	0.288
Insecta						
Coleoptera	2.0	0.001	2.0	0.011	2.0	0.192
Siphonophora	1.0	0.000	0.9	0.005	1.0	0.096
Algalmidae	8.0	0.002	6.6	0.035	8.0	0.768
Pisces						
Gonostomatidae						
Maurolicus muelleri	13,438.0	3.455	8,619.3	45.994	181.0	17.387
Synodontidae	8.0	0.002	16.0	0.085	3.0	0.288
Paralepididae	1.0	0.000	0.5	0.003	1.0	0.096
Myctophidae	43.0	0.011	62.3	0.332	5.0	0.480
Exocoetidae	2.0	0.001	2.0	0.011	2.0	0.192
Exocoetus volitans	1.0	0.000	56.0	0.299	1.0	0.096
Scomberesocidae						
Scomberesox saurus	8.0	0.002	105.0	0.560	6.0	0.576
Belonidae	2.0	0.001	5.0	0.027	2.0	0.192
Macrorhamphosidae	5.0	0.001	6.9	0.037	4.0	0.384
Sygnathidae	1.0	0.000	1.0	0.005	1.0	0.096
Holocentridae	3.0	0.001	4.0	0.021	1.0	0.096
Holocentrus sp.	3.0	0.001	9.0	0.048	1.0	0.096
Carangidae	1.0	0.000	1.0	0.005	1.0	0.096
Selene vomer	8.0	0.002	17.0	0.091	8.0	0.768
Decapterus punctatus	2.0	0.001	46.0	0.245	2.0	0.192
Caranx ruber	70.0	0.018	360.0	1.921	17.0	1.633
Mullidae	11.0	0.003	25.0	0.133	6.0	0.576
Scombridae	16.0	0.004	2.5	0.013	3.0	0.288
Auxis thazard	474.0	0.122	223.7	1.194	23.0	2.209
Scomber japonicus	1,474.0	0.379	978.7	5.223	77.0	7.397
Sarda sarda	81.0	0.021	127.0	0.678	8.0	0.768
Gempylidae	176.0	0.045	100.7	0.537	20.0	1.921
Thyrsitops lepidopoides	2,617.0	0.673	2,348.4	12.532	54.0	5.187
Trichiuridae	11.0	0.003	12.0	0.064	4.0	0.384
Benthodesmus sp.	19.0	0.005	80.9	0.432	8.0	0.768
Unid. Perciforms	24.0	0.006	63.7	0.340	16.0	1.537
Balistidae	1.0	0.000	5.0	0.027	1.0	0.096
Monacanthidae	27.0	0.007	19.8	0.106	19.0	1.825
Ostraciidae	1.0	0.000	0.5	0.003	1.0	0.096
Molidae						
Ranzania sp.	3.0	0.001	13.0	0.069	1.0	0.096
Triglidae	1.0	0.000	1.0	0.005	1.0	0.096
Peristedion sp.	1.0	0.000	1.0	0.005	1.0	0.096
Unid. fish	289.0	0.074	163.5	0.872	94.0	9.030
Unid. material	1.0	0.000	26.4	0.141	5.0	0.480
Empty					436.0	41.882
Total	388,912.0		18,739.9		1,041.0	

APPENDIX TABLE 2.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter I.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	112.0	0.0076	9.3	0.253	8.0	2.658
Lophogastridae	19.0	0.013	1.5	0.041	2.0	0.664
Isopoda	1.0	0.001	0.1	0.003	1.0	0.332
Flabellifera	1.0	0.001	0.1	0.003	1.0	0.332
Amphipoda	20.0	0.014	0.5	0.014	1.0	0.332
Euphausiidae	49.0	0.033	2.3	0.063	4.0	1.329
Euphausia similis	144,070.0	97.624	2,125.9	57.878	34.0	11.296
Caridea	1.0	0.001	0.5	0.014	1.0	0.332
Brachyura						
Unid. megalops	80.0	0.054	22.6	0.615	17.0	5.648
Unid. zooea	549.0	0.372	28.6	0.779	19.0	6.312
Unid. Decapoda	4.0	0.003	0.1	0.003	1.0	0.332
Unid. Crustacea	47.0	0.032	8.3	0.226	13.0	4.319
Mollusca						
Gastropoda						
Pteropoda						
Cavolina	68.0	0.046	2.2	0.060	1.0	0.332
Cephalopoda						
Teuthoidea	2.0	0.001	2.0	0.054	2.0	0.664
Thysanoteuthidae	2.0	0.001	10.0	0.272	1.0	0.332
Ommastrephidae	5.0	0.003	1.1	0.030	2.0	0.664
Loliginidae	1.0	0.001	8.0	0.218	1.0	0.332
Octopoda						
Argonautidae						
Argonauta sp.	2.0	0.001	0.3	0.008	2.0	0.664
Insecta						
Coleoptera	1.0	0.001	1.0	0.027	1.0	0.332
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,346.0	0.912	838.0	22.815	29.0	9.635
Belonidae	1.0	0.001	3.0	0.082	1.0	0.332
Holocentridae	3.0	0.002	4.0	0.109	1.0	0.332
Carangidae						
Selene vomer	6.0	0.004	9.0	0.245	6.0	1.993
Mullidae	2.0	0.001	8.0	0.218	1.0	0.332
Scombridae	15.0	0.010	1.5	0.041	2.0	0.664
Auxis thazard	427.0	0.289	189.7	5.165	21.0	6.977
Scomber japonicus	504.0	0.342	225.2	6.131	22.0	7.309
Gempylidae	76.0	0.051	48.5	1.320	11.0	3.654
Unid. Perciforms	9.0	0.006	7.0	0.191	5.0	1.661
Monacanthidae	13.0	0.009	9.5	0.259	8.0	2.658
Ostraciidae	1.0	0.001	0.5	0.014	1.0	0.332
Triglidae	1.0	0.001	1.0	0.027	1.0	0.332
Peristedion sp.	1.0	0.001	1.0	0.027	1.0	0.332
Unid. fish	137.0	0.093	76.5	2.083	35.0	11.628
Unid. material	1.0	0.001	26.3	0.716	4.0	1.329
Total	147,577.0		3,673.1		301.0	

APPENDIX TABLE 3.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter II.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	1.0	0.001	1.0	0.016	1.0	0.345
Mysidacea						
Eucopiidae	97.0	0.055	31.9	0.508	9.0	3.103
Lophogastridae	5.0	0.003	0.2	0.003	1.0	0.345
Isopoda						
Flabellifera	2.0	0.001	1.5	0.024	2.0	0.690
Amphipoda	2.0	0.001	1.0	0.016	1.0	0.345
Gammaridea	6.0	0.003	0.4	0.006	3.0	1.034
Euphausiidae	2.0	0.001	0.2	0.003	2.0	0.690
Euphausia similis	171,843.0	97.352	2,104.3	33.485	61.0	21.034
Caridea	1.0	0.001	0.8	0.013	1.0	0.345
Macrura						
Scyllaridae	1.0	0.001	0.2	0.003	1.0	0.345
Brachyura						
Unid. megalops	1.0	0.001	0.5	0.008	1.0	0.345
Unid. zooea	1.0	0.001	0.2	0.003	1.0	0.345
Unid. Decapoda	3.0	0.002	0.5	0.008	1.0	0.345
Unid. Crustacea	30.0	0.017	1.2	0.019	2.0	0.690
Mollusca						
Gastropoda						
Pteropoda						
Cavolina sp.	33.0	0.019	3.8	0.060	6.0	2.069
Cephalopoda						
Teuthoidea						
Ommastrephidae	6.0	0.003	8.5	0.135	5.0	1.724
Onychoteuthidae	13.0	0.007	6.0	0.095	2.0	0.690
Siphonophora						
Algalmidae	8.0	0.005	6.6	0.105	8.0	2.759
Pisces						
Gonostomatidae						
Maurolicus muelleri	4,287.0	2.429	3,548.0	56.458	38.0	13.103
Synodontidae	8.0	0.005	16.0	0.255	3.0	1.034
Myctophidae	24.0	0.014	61.3	0.975	4.0	1.379
Sygnathidae	1.0	0.001	1.0	0.016	1.0	0.345
Carangidae						
Selene vomer	2.0	0.001	8.0	0.127	2.0	0.690
Decapterus punctatus	2.0	0.001	46.0	0.732	2.0	0.690
Caranx ruber	70.0	0.040	360.0	5.729	17.0	5.862
Scombridae						
Auxis thazard	46.0	0.026	30.0	0.477	1.0	0.345
Scomber japonicus	8.0	0.005	6.0	0.095	2.0	0.690
Unid. Perciforms	1.0	0.001	12.0	0.191	1.0	0.345
Balistidae	1.0	0.001	5.0	0.080	1.0	0.345
Monacanthidae	4.0	0.002	4.1	0.065	3.0	1.034
Unid. fish	9.0	0.005	18.1	0.288	6.0	2.069
Total	176,518.0		6,284.3		290.0	

APPENDIX TABLE 4.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter III.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Mysidacea						
Eucopiidae	10.0	0.046	0.8	0.020	4.0	1.843
Isopoda						
Flabellifera	2.0	0.009	0.3	0.007	2.0	0.922
Euphausiidae	88.0	0.401	1.4	0.034	9.0	4.147
Euphausia sp.	50.0	0.228	0.6	0.015	1.0	0.461
Euphausia similis	15,414.0	70.236	196.3	4.796	30.0	13.825
Unid. Crustacea	5.0	0.023	0.4	0.010	4.0	1.843
Mollusca						
Cephalopoda						
Teuthoidea	1.0	0.005	3.0	0.073	1.0	0.461
Pisces						
Gonostomatidae						
Maurolicus muelleri	6,239.0	28.429	3,289.2	80.369	74.0	34.101
Exocoetidae	2.0	0.009	2.0	0.049	2.0	0.922
Exocoetus volitans	1.0	0.005	56.0	1.368	1.0	0.461
Macrorhamphosidae	2.0	0.009	2.9	0.071	2.0	0.922
Carangidae	1.0	0.005	1.0	0.024	1.0	0.461
Mullidae	6.0	0.027	9.0	0.220	3.0	1.382
Scombridae						
Scomber japonicus	45.0	0.205	374.0	9.138	8.0	3.687
Sarda sarda	6.0	0.027	4.0	0.098	2.0	0.922
Trichiuridae	11.0	0.050	12.0	0.293	4.0	1.843
Benthodesmus sp.	19.0	0.087	80.9	1.977	8.0	3.687
Unid. Perciforms	4.0	0.018	35.0	0.855	3.0	1.382
Monacanthidae	1.0	0.005	1.0	0.024	1.0	0.461
Unid. fish	39.0	0.178	22.8	0.557	21.0	9.677
Total	21,946.0		4,092.6		217.0	

APPENDIX TABLE 5.—List of prey items and other ingested materials found in the stomachs of skipjack tuna caught during Quarter IV.

Prey items	Numbers		Volume		Occurrence	
	No.	%	mL	%	No.	%
Crustacea						
Stomatopoda	11.0	0.026	3.5	0.075	5.0	2.146
Mysidacea						
Eucopiidae	1.0	0.002	0.4	0.009	1.0	0.429
Isopoda						
Flabellifera	2.0	0.005	0.2	0.004	2.0	0.858
Amphipoda						
Gammaridea	10.0	0.023	4.7	0.100	7.0	3.004
Euphausiidae						
Euphausia similis	37,305.0	87.017	468.8	9.996	47.0	20.172
Stylocheiron sp.	1.0	0.002	0.3	0.006	1.0	0.429
Caridea	1.0	0.002	1.0	0.021	1.0	0.429
Macrura						
Scyllaridae						
Unid. Phyllosoma larvae	1.0	0.002	0.1	0.002	1.0	0.429
Brachyura	5.0	0.012	0.7	0.015	1.0	0.429
Portunidae	1.0	0.002	0.1	0.002	1.0	0.429
Unid. megalops	21.0	0.049	8.9	0.190	9.0	3.863
Unid. zooea	5.0	0.012	1.4	0.030	4.0	1.717
Unid. Crustacea	14.0	0.033	1.1	0.023	7.0	3.004
Mollusca						
Gastropoda						
Pteropoda						
Cavoliniidae	1.0	0.002	0.1	0.002	1.0	0.429
Cephalopoda						
Teuthoidea	1.0	0.002	21.0	0.448	1.0	0.429
Ommastrephidae	24.0	0.056	45.5	0.970	11.0	4.721
Loliginidae	1.0	0.002	2.5	0.053	1.0	0.429
Histioteuthidae	1.0	0.002	1.0	0.021	1.0	0.429
Octopoda						
Argonautidae						
Argonauta sp.	18.0	0.042	75.6	1.612	9.0	3.863
Unid. Cephalopoda	4.0	0.009	1.3	0.028	3.0	1.288
Insecta						
Coleoptera	1.0	0.002	1.0	0.021	1.0	0.429
Siphonophora	1.0	0.002	0.9	0.019	1.0	0.429
Pisces						
Gonostomatidae						
Maurolicus muelleri	1,566.0	3.653	944.1	20.130	40.0	17.167
Paralepididae	1.0	0.002	0.5	0.011	1.0	0.429
Myctophidae	19.0	0.044	1.0	0.021	1.0	0.429
Scomberesocidae						
Scomberesox saurus	8.0	0.019	105.0	2.239	6.0	2.575
Belonidae	1.0	0.002	2.0	0.043	1.0	0.429
Macrorhamphosidae	3.0	0.007	4.0	0.085	2.0	0.858
Holocentridae						
Holocentrus sp.	3.0	0.007	9.0	0.192	1.0	0.429
Mullidae	3.0	0.007	8.0	0.171	2.0	0.858
Scombridae	1.0	0.002	1.0	0.021	1.0	0.429
Auxis thazard	1.0	0.002	4.0	0.085	1.0	0.429
Scomber japonicus	917.0	2.139	373.5	7.964	45.0	19.313
Sarda sarda	75.0	0.175	123.0	2.623	6.0	2.575
Gempylidae	100.0	0.233	52.2	1.113	9.0	3.863
Thyrsitops lepidopoides	2,617.0	6.104	2,348.4	50.074	54.0	23.176
Unid. Perciforms	10.0	0.023	9.7	0.207	7.0	3.004
Monacanthidae	9.0	0.021	5.2	0.111	7.0	3.004
Molidae	1.0	0.001	0.5	0.014	1.0	0.332
Ranzania sp.	3.0	0.007	13.0	0.277	1.0	0.429
Unid. fish	104.0	0.243	46.1	0.983	32.0	13.734
Unid. material	0.0	0.000	0.1	0.002	1.0	0.429
Total	42,871.0		4,689.9		233.0	

APPENDIX TABLE 6.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for all months. Data are $\bar{r} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(67)	9.51 ± 22.5	9.51 ± 25.4	42.50 ± 48.1	10.35 ± 29.5	8.57 ± 23.6	16.64 ± 36.4
50.0-54.9(155)	10.53 ± 27.7	12.62 ± 30.9	26.73 ± 43.6	13.99 ± 33.4	12.44 ± 29.5	20.05 ± 38.5
55.0-59.9(162)	24.81 ± 39.4	11.80 ± 29.5	20.40 ± 39.5	29.49 ± 43.6	5.62 ± 19.6	2.70 ± 14.2
60.0-64.9(147)	23.48 ± 39.2	8.03 ± 24.7	18.83 ± 36.5	42.90 ± 48.2	2.12 ± 12.2	—
65.0-69.9(55)	42.80 ± 47.6	12.43 ± 31.7	4.73 ± 18.7	32.18 ± 45.9	0.27 ± 2.0	—
70.0-74.9(13)	48.30 ± 48.1	9.88 ± 27.9	8.57 ± 21.9	23.36 ± 43.7	2.20 ± 79.2	—
75.0-79.9(4)	47.50 ± 55.0	27.50 ± 48.6	—	25.00 ± 50.0	—	—
Total (603)	18.80 ± 35.5	10.96 ± 28.6	22.22 ± 40.0	26.73 ± 42.8	6.24 ± 21.1	10.34 ± 27.9

APPENDIX TABLE 7.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter I. Data are $\bar{r} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(12)	28.70 ± 33.4	35.15 ± 42.5	9.18 ± 28.7	7.48 ± 25.9	13.89 ± 38.4
50.0-54.9(53)	19.87 ± 36.8	29.64 ± 43.5	24.48 ± 43.3	6.09 ± 19.6	16.12 ± 33.5
55.0-59.9(45)	30.23 ± 40.9	17.69 ± 33.9	20.81 ± 38.9	22.96 ± 38.1	7.98 ± 25.2
60.0-64.9(36)	34.79 ± 44.1	16.96 ± 35.4	20.14 ± 38.9	20.92 ± 40.1	19.84 ± 46.5
65.0-69.9(4)	48.61 ± 56.2	28.24 ± 47.9	—	—	3.71 ± 7.4
70.0-74.9(3)	91.67 ± 14.4	8.33 ± 14.4	—	—	—
75.0-79.9(2)	—	—	—	—	—
Total (155)	29.55 ± 41.0	23.47 ± 38.9	19.80 ± 38.9	14.18 ± 32.1	10.08 ± 27.3

APPENDIX TABLE 8.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter II. Data are $\bar{r} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(26)	1.65 ± 8.4	5.00 ± 20.3	76.92 ± 43.0	15.38 ± 36.8	—
50.0-54.9(12)	5.82 ± 11.5	14.72 ± 33.0	65.71 ± 48.6	—	—
55.0-59.9(35)	20.89 ± 38.7	18.13 ± 36.4	35.65 ± 49.9	14.71 ± 33.9	0.14 ± 0.80
60.0-64.9(45)	16.33 ± 36.2	4.67 ± 18.5	28.92 ± 45.7	45.54 ± 49.7	0.32 ± 2.1
65.0-69.9(23)	54.07 ± 49.1	—	4.49 ± 20.8	30.29 ± 46.8	—
Total (141)	20.02 ± 38.1	8.16 ± 25.2	38.32 ± 48.6	25.96 ± 43.3	0.14 ± 1.3

APPENDIX TABLE 9.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter III. Data are $\bar{r} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*
45.0-49.9(4)	25.81 ± 49.5	—	25.00 ± 50.0	24.19 ± 48.4	25.00 ± 50.0
50.0-54.9(27)	11.17 ± 32.0	1.24 ± 6.4	11.21 ± 32.0	61.56 ± 48.5	14.81 ± 36.2
55.0-59.9(36)	24.88 ± 41.3	9.22 ± 27.9	3.67 ± 16.2	59.05 ± 47.0	3.17 ± 16.8
60.0-64.9(31)	24.09 ± 40.5	3.39 ± 17.9	16.51 ± 29.9	53.76 ± 46.6	2.26 ± 12.6
65.0-69.9(17)	31.80 ± 46.4	17.65 ± 39.3	3.89 ± 9.8	46.67 ± 48.8	—
70.0-74.9(5)	31.27 ± 45.5	—	8.00 ± 17.9	60.73 ± 53.8	—
Total (120)	22.87 ± 40.1	6.42 ± 23.6	9.6 ± 25.5	55.40 ± 47.39	5.70 ± 22.7

APPENDIX TABLE 10.—Mean volumetric ratio of selected food items of skipjack tuna divided into 5 cm length groups for Quarter IV. Data are $\bar{r} \pm$ SD with (n) in parentheses. Range is 0-100%.

Length cm (n)	Other fish	Other crustaceans	*Euphausia similis*	*Maurolicus muelleri*	*Scomber japonicus*	*Thyrsitops lepidopoides*
45.0-49.9(25)	5.86 ± 13.8	3.43 ± 11.0	25.49 ± 39.6	4.26 ± 16.9	12.30 ± 25.1	44.60 ± 48.4
50.0-54.9(63)	3.30 ± 13.4	2.77 ± 13.0	27.84 ± 43.4	2.91 ± 16.3	10.69 ± 25.1	49.33 ± 47.0
55.0-59.9(46)	22.45 ± 37.5	3.25 ± 15.3	21.48 ± 40.2	24.01 ± 42.9	9.40 ± 22.5	9.49 ± 25.7
60.0-64.9(35)	20.51 ± 35.4	7.29 ± 22.1	6.55 ± 19.5	52.48 ± 49.9	1.71 ± 85.6	—
65.0-69.9(11)	34.11 ± 44.1	24.59 ± 40.2	8.26 ± 27.4	25.45 ± 43.9	—	—
70.0-74.9(5)	39.31 ± 53.8	20.69 ± 44.4	14.29 ± 31.9	—	5.71 ± 12.8	—
75.0-79.9(2)	45.00 ± 63.6	5.00 ± 7.1	—	50.0 ± 70.7	—	—
Total (187)	14.80 ± 16.5	5.6 ± 19.5	29.17 ± 37.8	19.31 ± 38.9	8.03 ± 21.2	24.91 ± 27.7

STOMACH CONTENTS OF YOUNG SANDBAR SHARKS, *CARCHARHINUS PLUMBEUS*, IN CHINCOTEAGUE BAY, VIRGINIA[1]

ROBERT J. MEDVED,[2] CHARLES E. STILLWELL,[3] AND JOHN J. CASEY[3]

ABSTRACT

During the summer of 1983 the stomach contents of 414 sandbar sharks captured by gill nets, and rod and reel fishing gear in Chincoteague Bay, Virginia, were examined. The blue crab, *Callinectes sapidus*, occurred in 67.4% of the stomachs and Atlantic menhaden, *Brevoortia tyrannus*, occurred in 13.3% of the stomachs. Other species of small crustaceans and fishes were found in < 6.0% of the stomachs, and 17.9% of the stomachs were empty. Data collected concerning the amount, stage of digestion, and number of food items in the stomachs indicated that feeding occurred during relatively short periods of time separated by long periods during which food was digested and no additional food was consumed. Sharks caught in gill nets were found to be in various stages of the feeding cycle and were more representative of the entire population than those caught by rod and reel. In the stomachs of these sharks, crustaceans accounted for nearly twice as much of the mean weight of food as did fish. The mean quantity of food in the stomachs was 0.96% of body weight (BW) and the maximum quantity was 5.28% of BW. The quantity of food in all stomachs was significantly less than the estimated maximum stomach capacity (13.0% BW). Sharks caught between 0130 and 0430 were found to contain considerably more food in their stomachs than sharks caught during other times of the day. The data collected from this study when combined with information concerning gastric evacuation will provide the basis for food consumption estimates in this species.

Traditionally the management of commercially valuable fisheries has been based on single-species production models and the concept of maximum sustainable yield (Hennemuth 1979). Although generally accepted as an objective of management, the estimation and application of maximum sustainable yield have not provided satisfactory results and have, in fact, led to significant declines of some traditional and highly valued fisheries (Edwards and Hennemuth 1975; Hennemuth 1977; Holt and Talbot 1978). The poor results of single-species models in allocating fishing quotas may be due in part to the fact that they assume no interactions of the target species with other components of the ecosystem. In recent years it has become clear that this assumption is unrealistic and that variables such as competition, predation, and abiotic factors should be considered in any assessment of fishery productivity and potential yields to man. It has been pointed out (Gulland 1978, 1983; Mercer 1982) that the future success of our attempts at managing fishery resources will depend, to a large extent, on our ability to develop multispecies production models that adequately account for interactions among species. An important component of these models is predator-prey interactions. In fact, collection of data on the diets of the major predators is considered absolutely necessary for the progress of multispecies assessment techniques (Hennemuth 1980[4]; Mercer 1982). Considering their position as one of the most abundant apex predators in the sea, predation by sharks undoubtedly plays a major role in the exchange of energy in the marine environment. In fact, a study by Jones and Geen (1977) has indicated that the spiny dogfish, *Squalus acanthias*, in British Columbia waters annually consumes over 5 times the commercial catch of herring and up to 44% of the total stock. The impact that sharks have on commercial fisheries can only be determined by knowing the diversity of prey items and the biomass of each consumed. While numerous publications on sharks incorporate lists of items found in their stomachs, very little is known about daily ration and the amounts of food consumed annually.

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[2]University of Rhode Island, Graduate School of Oceanography, Narragansett, RI; present address: Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882.

[3]Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882.

[4]Hennemuth, R. C. 1980. Research needs for multispecies fisheries. Office of Technology Assessment Workshop, Seattle, WA., 21-23 April.

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In most investigations the food consumption of fishes has been studied by methods that involve laboratory techniques to estimate various parameters relating to growth, metabolism, digestion, and excretion (reviews by: Davis and Warren 1971; Mann 1978). These methods, however, are of limited value for fishes such as sharks that are difficult to maintain in captivity. An alternate method for determining food intake that can be applied to fishes in the wild has been successfully used in several studies (Bajkov 1935; Swenson and Smith 1973; Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981; Stillwell and Kohler 1982; Durbin et al. 1983). This approach requires information concerning the quantity of food found in the stomachs of fishes sampled at regular intervals over 24-h periods and the rate at which food is evacuated from the stomach. The objective of the present study was to obtain the quantitative stomach content data needed to use this approach to estimate the daily food ration of the sandbar shark, *Carcharhinus plumbeus*. The sandbar shark was selected for this study because it is one of the few sharks for which gastric evacuation data are available (Medved in press). It is also an abundant, widely distributed shark (Springer 1960; Casey 1976) known to feed on commercially valuable species (Medved and Marshall 1981). In addition, it is a member of a large family of sharks (Carcharhinidae) and data collected for this species will provide the basis for making preliminary estimates of food consumption for the other members of the family.

METHODS

During the summer of 1983, young sandbar sharks were collected from Chincoteague Bay, VA, for stomach content analysis. The study area is located within the summer distribution of this species and supports a relatively large number of young sandbar sharks from early June through September. The bay is about 40 km long and 8 km wide at its widest point, and the average water depth is 2 m. A tidal inlet connects the bay with the Atlantic Ocean, and the tidal range varies from 0.75 to 1.50 m. The area is also characterized by strong tidal currents, vast salt marshes, and brackish to seawater salinities.

A 4.9 m outboard motor boat was used as a fishing platform, and sharks were caught using monofilament gill nets and rod and reel fishing gear. The gill nets were 91 m long, 1.8 m deep, and had a stretched mesh size of 10.8 cm. They were anchored at both ends and were buoyed so the foot rope touched the bottom. Net retrieval was made every 1 to 2 h. The fishing rods were equipped with Penn[5] reels of 3/0 size, and the terminal tackle consisted of two wire leaders, each with a 4/0 fishing hook baited with squid. The hooks were set 1 m off the bottom. Both types of gear were used during all hours of the day. Upon capture each shark was brought into the boat where it was sexed, measured, and weighed. The sharks were then cut open and the stomach contents were removed and stored on ice in plastic bags.

In the laboratory each food item was identified to species and a length measurement was made when possible. Each item in the stomach was also assigned a stage-of-digestion value ranging from 1 to 6 with a higher number indicating a greater extent of digestion. The stage-of-digestion scale was based on a gastric evacuation study (Medved in press) in which sandbar sharks were fed preweighed meals of either blue crab, *Callinectes sapidus*, or Atlantic menhaden, *Brevoortia tyrannus*, and were maintained in an enclosure constructed in the natural environment. The range of water temperatures in the enclosure (22.0°-30.0°C) was close to that recorded during the present study (20.0°-27.3°C). The sharks were sacrificed at various time intervals after feeding, and the food remains were weighed and described. The food item descriptions were used to arbitrarily establish six stages of digestion that were each one-sixth of the total evacuation time. Each stage of digestion was about 12 h long for crustacean prey and 15 h long for fish prey. After identification of food items and assignment of digestion values, the stomach contents of each shark were separated into fish and crustacean components that were weighed to 0.01 g after draining off excess water. Each sample was then dried at 80°C to constant weight (about 72 h) and again weighed to 0.01 g.

RESULTS

During the study 414 sharks were captured for stomach content analysis. The numbers of sharks caught by each fishing method and during various time periods of the day are summarized in Table 1. The number of male and female sharks collected was nearly equal (210 and 204 respectively), and they ranged in size from 40.0 to 80.0 cm fork length (FL) ($\bar{x}$ = 56.1, SD = 6.8). Body weights were obtained from 369 (89.1%) of these sharks, and ranged from 720.0 to 5,690.0 g ($\bar{x}$ = 1,885.5, SD = 738.8). The body weight of the sharks not weighed was estimated from a regression equation derived from the

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of sharks caught for stomach content analysis during different time intervals and by the two capture methods.

Time interval	Rod and reel	Gill net	Total
2230-0130	19	33	52
0130-0430	11	27	38
0430-0730	20	20	40
0730-1030	21	27	48
1030-1330	27	27	54
1330-1630	39	39	78
1630-1930	18	30	48
1930-2230	23	33	56
Total	178	236	414

animals that were measured and weighed: $Wt = 0.0123\ (FL)^{2.9577}$ ($n = 369$, $R^2 = 0.97$). Water temperature during the fishing periods ranged from 20.0° to 27.3°C ($n = 172$, $\bar{x} = 25.1$) but 90% of the temperatures were between 23.9° and 26.4°C.

Fifteen different food types were identified in the stomachs (Table 2). A relatively large number of stomachs ($n = 74$, 17.9%) were empty, and unidentifiable fish remains occurred in others ($n = 21$, 5.1%). The blue crab was the most frequently occurring food item and was found in 279 (67.4%) of the stomachs examined and in 82.1% of the stomachs containing food. Of the food remains that could be positively identified as individual blue crabs ($n = 309$), 88.0% of the crabs had recently molted and were soft. The crabs that could be measured ranged in size from 1.0 to 14.0 cm between the two points of the carapace ($n = 136$, $\bar{x} = 7.4$). Although exact numbers were difficult to determine, it appeared that less than half of the blue crabs were consumed whole. The only other prey frequently found was the Atlantic menhaden, which occurred in 55 (13.3%) of the stomachs examined and in 16.2% of the stomachs with food. Of the 61 cases where it was possible to determine if the fish was consumed whole or in part, 28 (45.9%) of the menhaden were whole and ranged in size from 5 to 10 cm total length (TL) ($\bar{x} = 7.3$). The estimated sizes of the partially eaten menhaden ranged from 5 to 17 cm TL ($\bar{x} = 8.6$). All other prey items were found in < 6.0% of the stomachs examined.

The distributions of stage-of-digestion values assigned to the food items in the stomachs of sharks caught by the two different fishing methods are shown in Figure 1. The distribution for sharks caught by rod and reel indicated that 71.8% of the food items were in either the first or last stage of digestion. In contrast, food items in the stomachs of sharks caught by gill nets were divided more evenly among all the stages of digestion. The two capture methods also differed in the proportion of sharks

TABLE 2.—Stomach contents found in a sample of 414 sandbar sharks.

Stomach content	No. of stomachs found in	Percent of stomachs found in
Blue crab, *Calinecties sapidus*	279	67.4
Empty	74	17.9
Atlantic menhaden, *Brevoortia tyrannus*	55	13.3
Summer flounder, *Paralichthys dentatus*	24	5.8
Unidentified fish	21	5.1
Mantis shrimp, *Squilla emprisa*	18	4.4
American eel, *Anguilla rostrata*	15	3.6
Spot, *Leiostomus xanthurus*	14	3.4
Atlantic silverside, *Menidia menidia*	9	2.2
Smooth dogfish, *Mustelus canis*	7	1.7
Northern pipefish, *Syngnathus fuscus*	6	1.5
Anchovy, *Anchoviella mitchilli*	5	1.2
Squid, *Loligo pealei*	5	1.2
Bluefish, *Pomatomus saltatrix*	3	0.7
Calico crab, *Ovalipes ocellatus*	1	0.2
Mummichog, *Fundulus heteroclitus*	1	0.2
Northern seahorse, *Hippocampus hudemius*	1	0.2

caught with empty stomachs. The percentage of the 178 sharks caught by rod and reel with empty stomachs (22.5%) was significantly higher than that found for the 236 sharks caught by gill nets (14.4%; z-test, $P = 0.015$).

Of the 414 stomachs examined, 203 contained a single food item. A stage-of-digestion value of 5 or 6 was assigned to 89 (43.8%) of these items, indicating that many sharks went at least the time equivalent of 5 stage-of-digestion units between meals (48 to 60 h for crustacean prey or 60 to 75 h for fish prey).

Multiple food items were found in 137 stomachs. The difference between the stage-of-digestion values

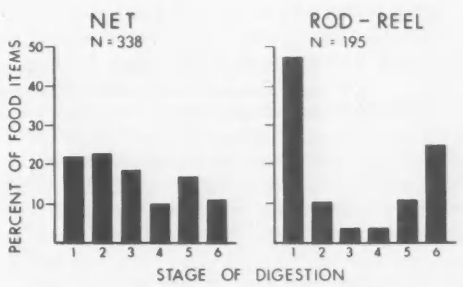

FIGURE 1.—Distributions of stage-of-digestion values assigned to food items present in the stomachs of sharks caught with gill net and rod and reel.

of the first and last eaten food items within each stomach was calculated to assess the amount of time that passed during consumption of multiple item meals. In 19 stomachs a food item in the sixth stage of digestion and one in the first stage of digestion were found. In these cases a time equivalent of 5 stage-of-digestion units had passed between consumption of the two food items, and since a stomach containing an item in stage 6 of digestion would be relatively empty, the two food items were considered to represent two different meals. Excluding the above 19 stomachs from analysis, the mean difference between the stage-of-digestion values of the first and last eaten food items was calculated for stomachs containing from 2 to 5 items (Table 3). The overall mean difference was 0.60 stage-of-digestion units indicating that multiple food items in the stomachs were in similar stages of digestion.

The quantity of food in each stomach examined was measured on a wet weight and dry weight basis. Excluding empty stomachs from analysis, the total dry weight of food (TDW) was found to be linearly related to the total wet weight of food (TWW) in the stomachs (TDW = $-0.24 + (0.22)$ TWW; $n = 318$, $R^2 = 0.96$). Since the two measurements were highly correlated ($r = 0.98$) and wet weight measurements have frequently been used in similar food studies on other species, it seemed valid to express the food quantity results in this paper on a wet weight basis. Table 4 summarizes the descriptive statistics of the quantity of food in 414 stomachs examined. The mean total weight of food found in the stomachs of sharks caught by gill nets was significantly higher than that found for sharks caught by rod and reel (18.91 and 13.09 g respectively; z-test, $P = 0.003$). Similar results were obtained when food quantity was measured as a percentage of shark body weight (0.96 vs. 0.76%; z-test, $P = 0.043$). This result, in conjunction with the other differences between the two capture methods mentioned above, suggested that sharks caught by rod and reel may not have been representative of the entire population (see section on Discussion). Because the primary value of the stomach content data in this study will be in the estimation of food consumed by the population, the following results concerning the amount of food in the stomachs were based on sharks caught by gill nets since they were probably more representative of the entire population of young sandbar sharks in the study area. For sharks caught by gill nets, crustaceans accounted for nearly twice as much of the mean total wet weight of food in the stomachs than did fish. The mean wet weight of crustaceans in the 236 stomachs (12.37 g) was significantly higher than the mean of 6.53 g found for fish (z-test, $P < 0.001$). Similar results were obtained when food quantity was expressed as a percentage of shark body weight (0.65 vs. 0.31%; z-test, $P < 0.001$). The mean weights of the two food components in the stomachs

TABLE 3.—Number of stomachs for which the stage-of-digestion value of the first eaten food item minus the stage-of-digestion value of the last eaten food item was equal to the given difference. The data are broken down into groups based on the number of food items present in the stomachs. Stomachs that contained an item at stage 1 of digestion and an item at stage 6 of digestion are not included (see text).

No. of items in stomach	No. of stomachs with indicated difference between stage-of-digestion values of first and last food items eaten							
	Difference						Mean difference	SD
	0	1	2	3	4	*N*		
2	44	25	9	0	1	79	0.60	0.78
3	13	17	0	0	0	30	0.57	0.50
4	2	3	2	0	0	7	1.00	0.76
5	2	0	0	0	0	2	0	0
Overall	61	45	11	0	1	118	0.60	0.78

TABLE 4.—Summary statistics of the amount of food in the stomachs of a sample of 414 sandbar sharks. Sharks were captured with gill nets and rod and reel gear. The z-test statistic was used to test the equality of the indicated pairs of mean values.

Stomach contents	Capture method	Mean	*N*	SE mean	Max	Min	z-test stat.	P-value 2-tailed test
Fish (g)	Gill net	6.53	236	1.10	114.80	0	3.74	< 0.001
Crustacea (g)	Gill net	12.37	236	1.11	102.20	0		
Fish (% BW)	Gill net	0.31	236	0.04	3.93	0	4.84	< 0.001
Crustacea (% BW)	Gill net	0.65	236	0.06	5.28	0		
Total (g)	Gill net	18.91	236	1.53	135.68	0	2.95	0.003
Total (g)	Rod and reel	13.09	178	1.25	100.30	0		
Total (% BW)	Gill net	0.96	236	0.06	5.28	0	2.02	0.043
Total (% BW)	Rod and reel	0.76	178	0.07	6.92	0		

were also calculated for each of eight consecutive 3-h time intervals of the day (Fig. 2). The means ranged from 1.05 to 14.92 g for fish, from 7.51 to 19.72 g for crustaceans, and from 11.74 to 34.64 g for the total wet weight of food in the stomachs. When 95% confidence bounds were placed around the means, considerable overlap of the confidence intervals was observed (Fig. 2). However, the mean total wet weight in the stomachs of sharks captured between the time of 0130 and 0430 was considerably higher than the other means, and the confidence interval for the mean during this time period overlapped substantially with only two of the remaining seven intervals. Similar results were obtained when food quantity was expressed as a percentage of shark body weight.

During the study one stomach was examined that contained a total wet weight of 444.0 g of food (10.3% BW (body weight)). This shark was not included in the results presented above because the quantity of food in the stomach was substantially greater than for any other shark. It is mentioned here because it does indicate that the stomach capacity of this species is considerably greater than the amount of food typically found in the stomach. In an attempt to estimate maximum capacity, the stomachs of 23 sharks were removed, ligated, and filled with water to the point at which they were about to burst. This point was determined by filling several stomachs until they burst and noting the changes that occurred in the stomach wall just before the bursting point. The average maximum capacity of the stomachs was found to be 13.0% of BW (range: 8.04 to 19.8%). For sharks caught by gill nets the mean quantity of food in the stomachs (0.96% BW) was 7.4% of maximum capacity and the largest quantity of food in a stomach (5.28% BW) was 40.6% of maximum capacity.

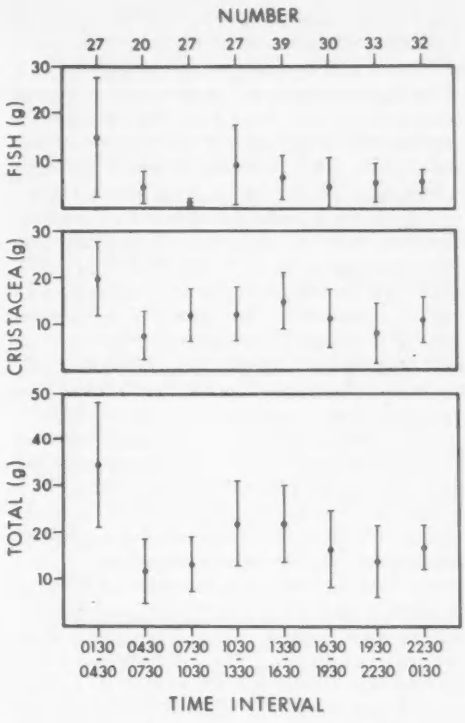

FIGURE 2.–Amount of food in the stomachs of sandbar sharks caught by gill nets during various time intervals of the day. Dots indicate mean wet weight in grams, and bars represent 2 standard errors on each side of the mean. The number of stomachs examined during each interval is given at the top of the figure.

DISCUSSION

Several investigations conducted in other areas have reported the sandbar sharks' diet to consist of small crustaceans and fish (Bigelow and Schroeder 1948; Springer 1960; Clark and von Schmidt 1965; Bass et al. 1973; Lawler 1977). With the exception of squid in several stomachs, the prey items of the sandbar sharks captured in Chincoteague Bay, VA, were also found to be small crustaceans and fish (Table 2) and agree with those reported by Medved and Marshall (1981) for this species in Chincoteague Bay. The studies above provided little specific information concerning the frequency of occurrence, size, relative amounts, or physical state of the food items. In the present study, small blue crabs that had recently molted were, by far, the predominant food item in terms of both weight and numbers. Small menhaden were also found to comprise a significant portion of the food consumed, but other species appeared to be of minor importance in the diet of the sandbar shark in the study area.

The results of this study strongly suggest that the feeding behavior of sandbar sharks in the study area was characterized by relatively short periods of feeding activity separated by substantially longer periods of time during which stomach contents were digested and no additional feeding occurred. An indication that this species may go relatively long periods of time without feeding was the high percentage (21.5%) of sharks that had a single food item in their stomach that was in a late stage of digestion (stage 5 or 6). Based on the approximate duration of each

stage of digestion (12 or 15 h depending on prey type) these sharks apparently had gone at least 48 h without consuming additional food. Another 17.9% of the sharks captured had empty stomachs. None of these were found to have an everted stomach, indicating that regurgitation of food was not responsible for the high percentage of empty stomachs. Additionally, 98 sandbar sharks fed preweighed meals and released in an enclosure in the natural environment were not observed to regurgitate food when recaptured at a later time (Medved in press). Thus it appears that the sharks with empty stomachs had not consumed food for a period of time greater than the time required to evacuate the last meal (at least 72 h). Given the long duration of gastric evacuation, a shark feeding nearly continuously would have many food items at various stages of digestion in the stomach. Multiple food items were found in some stomachs, but 90.6% of the stomachs contained less than three food items. Multiple food items in a stomach were also generally in similar stages of digestion (Table 3). The sharks with a single food item in their stomach consumed that meal in a very short period of time. The mean difference between the stage-of-digestion values of the first and last prey item consumed by sharks with multiple items in their stomach was 0.60 units (Table 3). Considering that digestion was divided into six stages, the feeding duration of sharks that consumed a meal of multiple food items was also very short relative to the time required for complete gastric evacuation. Observations made during a study of gastric evacuation in the sandbar shark also suggested that feeding ceased after the consumption of a meal (Medved in press). In that study the stomachs of 98 sharks were lavaged to remove all food and a preweighed meal was then fed to each animal. The sharks were released in a large enclosure in the natural environment that contained an abundance of prey and were recaptured at various times after feeding. Of the 54 sharks sacrificed within 40 h of feeding, only 4 had consumed additional food. In contrast, of 11 sharks that had their stomachs lavaged but were not fed a meal before release all but 2 were found to have food in their stomachs when sacrificed 24 h later. The results discussed above indicate that the feeding activity of sandbar sharks in the study area was intermittent rather than continuous. Similar models have been proposed in several other feeding behavior studies on fishes. Diana (1979) proposed an intermittent feeding model for the northern pike, *Esox lucius*, and suggested that such a model was appropriate for many top carnivores. Longval et al. (1982) have shown that after captive lemon sharks, *Negaprion brevirostris*, have fed to satiation, it takes a few days for the appetite to become reestablished. Carey et al. (1982) suggested that the great white shark, *Carcharodon carcharias*, may maintain itself for more than a month on a single large meal. Holden (1966) and Jones and Geen (1977) indicated that the spiny dogfish, *Squalus acanthias*, consumes a meal and then ceases to feed until digestion is complete. Observations made by Sano (1959) suggest that this may be typical of other shark species as well.

The differences observed between the stomach contents of sharks caught by the two capture methods are consistent with the model of feeding postulated above. The majority of sharks caught by rod and reel had stomachs that were empty or that contained food items in the first or last stage of digestion (Fig. 1). The sharks with empty stomachs had apparently not consumed food for a long period of time. Those with a food item in the last stage of digestion had relatively empty stomachs and had also gone a considerable time without feeding. Finally, the sharks with a food item in the first stage of digestion had eaten within several hours of being caught. Assuming that these sharks were actively feeding since they were inclined to consume the squid used as bait, it appears that the sharks in a "feeding mode" were those with relatively empty stomachs that had not fed for some time and those that had just eaten but were inclined to consume additional food. The stomachs of sharks caught by gill nets were empty or contained a single food item or multiple food items in similar stages of digestion suggesting, as indicated above, that feeding was intermittent. However, the stage-of-digestion values of the food items in the stomachs were spread more evenly over the digestion scale than for sharks caught by rod and reel, indicating that these sharks were in various stages of the feeding cycle (Fig. 1). The higher percentage of empty stomachs and lower mean stomach content weight found for sharks caught by rod and reel than for those caught by gill nets also suggested that sharks caught by rod and reel were those in a "feeding mode" and that sharks caught by gill nets were probably more representative of the entire population.

For sharks caught by gill nets the mean quantity of food in the stomach was 0.96% of BW and the maximum quantity was 5.28% of BW (Table 4). Considering that the mean stomach content was based on sharks containing food in various stages of digestion, it probably is a significant underestimation of the average meal size of sharks in the area. In contrast, the maximum quantity of food found in a stomach is undoubtedly an overestimate and the

average meal size should be considered to have been somewhere between the two values. It would then appear that the average meal size of the sharks captured was substantially less than the estimated stomach capacity (13.0% BW). The mean stomach content weights found for various time intervals of the day in this study suggested that sandbar sharks contained more food in their stomachs between 0130 and 0430 than during other times of the day (Fig. 2). The evidence was not overwhelming but these results do agree with a study by Medved and Marshall (1981), indicating that night hours may be a period of increased feeding activity for the sandbar shark.

Although this paper has provided a quantitative description of the stomach contents of the sandbar shark, data concerning stomach contents alone are not sufficient for estimating food consumption. As pointed out by numerous researchers, the amount of food in a fish's stomach is a function of both the rate of ingestion and the rate of gastric evacuation (Eggers 1977; Thorpe 1977; Elliott and Persson 1978; Jobling 1981). However, when combined with detailed information concerning gastric evacuation, the results of this study will provide the basis for the construction of an appropriate model of food consumption for the sandbar shark.

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THE SPAWNING CYCLE OF SOFT-SHELL CLAM, *MYA ARENARIA*, IN SAN FRANCISCO BAY

SHELLY E. ROSENBLUM AND THOMAS M. NIESEN[1]

ABSTRACT

Four populations *Mya arenaria* in San Francisco Bay were studied for 1 year to determine the spawning cycle. The spawning cycle was well synchronized among the four populations. Gametogenesis had commenced by late February and spawning occurred uninterrupted from April through summer. Cessation of spawning occurred from September to October. The protracted spawning period of *M. arenaria* populations in San Francisco Bay is probably related to the long period of moderate water temperatures (March-October) which occur there. Size at first reproduction was placed at a shell length of 25 mm. Sex ratios of *M. arenaria* > 25 mm in shell length did not differ significantly from 1:1. No evidence of hermaphroditism was observed.

The soft-shell clam, *Mya arenaria*, was once popular with clam diggers in San Francisco Bay. During the early 20th century, owners of bay front property fenced off portions of the mud flats in order to exclude clam predators, thus insuring bountiful harvests of *M. arenaria* (Bonnot 1932). Today as the "trend toward the improvement of San Francisco Bay water continues,"[2] the potential for a recreational shellfishery exists again. Agencies for communities on the bay have begun to look at this potential. Recently (1982), the digging of clams in San Francisco Bay received official clearance for the first time in 30 yr.[3]

The spawning cycle of the soft-shell clam has been studied extensively on the east coast. Ropes and Stickney (1965) examined populations from the Cape Cod-New England region. They did not encounter clams in the ripe stage of gametogenesis until May, and by September spawning was over. Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning occurred between March and April and was of short duration. A separate, second spawning took place from June through July. Porter (1974) studied *M. arenaria* from populations at Skagit Bay, WA. He noted a single yearly spawning from late May to early September.

The climate of the San Francisco Bay area, and hence the seasonal water temperature fluctuations of San Francisco Bay, are much less extreme than that of the New England or Washington areas and most of the other locations from which *M. arenaria* has been examined. The question investigated in this study is whether the spawning cycle of *M. arenaria* from San Francisco Bay would differ from that of other areas reported in the literature.

MATERIALS AND METHODS

Description of Study Sites

Specimens of *M. arenaria* were collected from September 1979 through December 1980 from four sites around central San Francisco Bay (Fig. 1): 1) Candlestick Point – adjacent to the causeway leading to the Candlestick Park Stadium (lat. 37°42′32″N, long. 122°23′28″W); 2) Burlingame Lagoon – just south of San Francisco International Airport (lat. 37°35′12″N, long. 122°20′10″W); 3) Foster City – immediately north of the San Mateo Bridge, off Third Street (lat. 37°34′20″N, long. 122°23′28″W); 4) Point Isabel – north of the Golden Gate Fields race track on the eastern shore of San Francisco Bay (lat. 37°53′59″N, long. 122°23′28″W). These areas were selected because they experience annual variations in temperature and salinity (Conomos 1979), factors which are known to affect bivalve spawning cycles (Loosanoff and Davis 1951; Swan 1952; Matthiessen 1960, Pfitzenmeyer 1962; Stickney 1964). Substratum conditions were classified according to field observations; no particle size analyses were conducted.

[1]Department of Biological Sciences, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132.

[2]Jones and Stokes Associates, Inc. 1977. San Francisco Bay shellfish: an assessment of the potential for commercial and recreational harvesting. Prepared for the Association of Bay Area Governments, 171 p.

[3]Champion, D. 1982. Clam digging OK'd on part of San Francisco Bay. San Francisco, Chronicle, 27 August 1982, p. 1.

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The Candlestick Point site has a sandy substratum and is adjacent to a broad expanse of mud flat. Temperatures and salinities at this site reflect those of the central San Francisco Bay (Conomos 1979). Clams were collected high on the sandy beach front 0.6 m above Mean Lower Low Water (MLLW) in the areas exposed as the tide begins to recede.

Burlingame Lagoon is separated from San Francisco Bay by a levee with a narrow channel connecting to the open body of the Bay (Fig. 1). Salinity and temperature can vary dramatically with heavy rains (8 to 12 ppt) (pers. obs.). The area has a heavy clay-mud substratum. The collecting site was 0.6 m above MLLW.

The Foster City site was selected because it reflects conditions more closely associated with the south bay (Conomos 1979). The substratum is sandy-mud with rocks and cobble intermixed. The area juts into the bay and is exposed to wave action and temperatures and salinities characteristic of the bay waters (Conomos 1979). It is adjacent to outflow from the tidal channel that winds through Foster City. The collecting site was 0.24 m above MLLW.

The Point Isabel site is on the mud banks of a narrow (4 m wide) tidal channel that bisects the Point Isabel promontory. The substratum is clay-mud with rock and debris intermixed. Clams were collected from 0.15 to 0.46 m above MLLW.

The depths of the collection sites (relative to MLLW) at the four locations were dictated by the presence of *M. arenaria* at each site. *Mya arenaria* signals its presence by distinct siphon holes at the surface of the substratum. After an initial excavation of each collection site to a depth of 10 cm, it became obvious that clams were present only in the specific areas clearly marked by their siphon holes. Thereafter only these areas were sampled.

Temperature and salinity were recorded with a field hydrometer (marked at ppt) and thermometer at each site each month, beginning in October 1979 and continuing through November 1980.

Collecting Methods

A gardener's hand rake and careful hand digging was used for excavating the deep-dwelling *M. arenaria*. At least 25 clams were collected from each of the four sites each month for 1 yr (with the following exceptions: 4 October–Foster City, 12 collected; 3 November–Foster City, 20 collected; 25 December–Foster City, 24 collected; 2 November–Candlestick Point, 20 collected; 24 September–Point Isabel, 20 collected; 3 November–Burlingame, 7 collected). A total of 1,625 clams were examined in this study. Clams were collected, placed in a Thermos[4] jug of cool bay water, and returned to the laboratory.

Processing Methods

Analysis of gonadal stage was made by microscopical examination of histological preparations (Ropes and Stickney 1965). The presence and development of gametes was used to infer the spawning stage or readiness of the clam. Specimens were measured for shell length to the nearest 0.1 mm. The anterior one-third of the visceral mass (Ropes and Stickney 1965) was removed, labeled, and placed in Bouin's seawater fixative. During dissection, tissues were submerged in cool seawater to prevent drying or osmotic changes. The time between collection and preservation was under 3 h to prevent any gonadal changes.

The tissues were subjected to standard histological procedures (dehydrated in alcohol and embedded in paraffin). Embedded tissues were thin sectioned (5 μ) on a rotary microtome. Sections were mounted on glass slides, stained with Harris' hematoxylin and eosin, and examined using standard light microscopy.

Each slide of gonadal tissue was studied to determine the presence of male or female gametes and the condition of the gonadal tissues. This allowed clams to be placed into one of the five classes of spawning readiness (inactive, active, ripe, partially spawned, spent) employed and described by Ropes and Stickney (1965) for *M. arenaria*.

Categories of Spawning Readiness (adapted from Ropes and Stickney 1965)

Female Gonads

INACTIVE PHASE.–Ropes and Stickney (1965) used the term "inactive" to describe this phase. Brousseau (1978) preferred the term "indifferent" because cellular activity is continuing although no gametogenic activity is obvious. The term "inactive" is employed here and refers to individuals which are not seen to be producing gametes whether due to seasonal quiescence or immaturity. Thus in this research which presents pooled male and female data, the "inactive phase" may contain sexually undifferentiated individuals along with inactive animals clearly recognizable as male and female.

Females in the inactive phase exhibit small oocytes

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

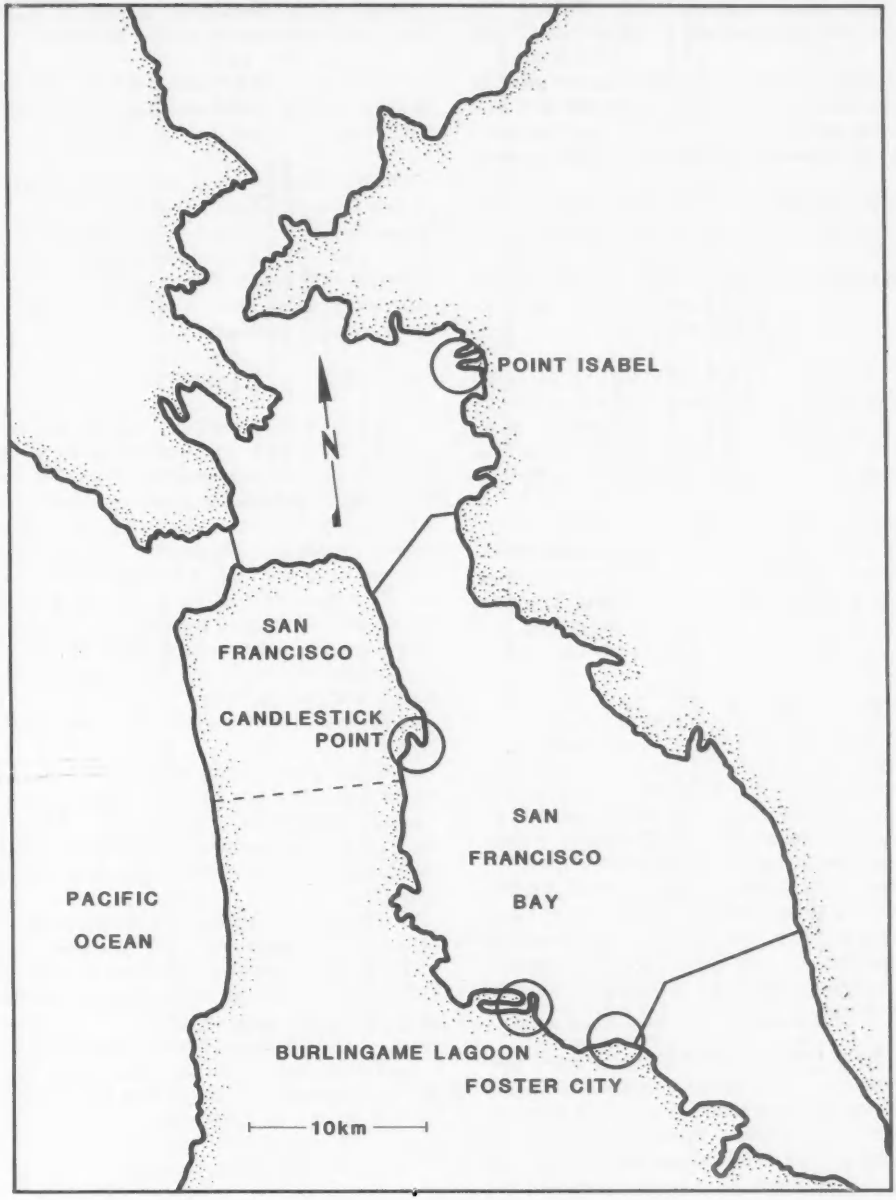

FIGURE 1.–Study sites on San Francisco Bay indicated by circles.

at the periphery of alveoli. Follicle cells completely imbed the oocytes and may fill the lumina of alveoli.

ACTIVE PHASE.–Enlarging oocytes grow between follicle cells towards the center of alveoli. Oocytes are irregular in shape but are attached to the wall of the alveolus by broad cytoplasmic bases.

RIPE PHASE.–In the ripe phase, oocytes appear as round cells in the lumina of the alveoli as if free of attachment to the basal membrane, yet they may be attached by a very slender stalk. The large oocytes fill the lumina of the alveoli and are usually more numerous than less developed oocytes.

PARTIALLY SPAWNED PHASE.–Gonadal tissues contain a few ripe oocytes. Small oocytes are imbedded in follicle cells at the periphery of an empty alveolus. Many alveoli are devoid of ripe oocytes.

SPENT PHASE.–Very few ripe oocytes are present, usually darkly staining with obscure nuclei. Numerous spherical droplets of lipoids and other products of cytolysis are characteristic. The spent phase progresses into the inactive phase.

Male Gonads

INACTIVE PHASE.–During the inactive phase, male tissues contain products of atypical spermatogenesis (Coe and Turner 1938). Tissues appear quite active, yet this activity will not result in viable male gametes. Pycnotic cells and multinucleated cells appear in the follicles. A few spermatogonia and primary spermatocytes may be seen at the periphery of alveoli while aberrant cells can be seen throughout the alveoli. As indicated in the description of the inactive phase for female gonads, this phase category is expanded to include sexually undifferentiated individuals along with pooled male and female inactive phase animals.

ACTIVE PHASE.–Proliferating primary spermatocytes exist at the basal membrane of the alveoli. These are small and uniformly sized cells which are similar to the earliest oocytes. They can be seen growing between follicle cells, extending toward the centers of the alveoli. Early stages of meiosis occur at the periphery of the alveoli, while later spermatids occur at the alveolar centers where they later form a distinct mass. Follicle cells eventually disappear.

RIPE PHASE.–Masses of spermatozoa arranged in more or less radial columns exist in rounded alveoli with tails oriented toward the center.

PARTIALLY SPAWNED PHASE.–Relatively few spermatozoa can be seen. Follicle cells start to refill the alveoli. Some pycnotic cells occur.

SPENT PHASE.–Spent male tissues contain no or very few spermatozoa in the central alveolar area. Numerous follicle cells with multinucleated cells and pycnotic cells from atypical spermatogenic activities surround small groups of spermatozoa. Tissues lack cells in the active phase of spermatogenesis. The spent phase progresses into the inactive phase.

RESULTS

Of the 1,674 clams examined in this study, 1,361 were distinguishable as male or female; the remaining 313 were indistinguishable as to sex. The male: female ratio (670:691) did not vary significantly from a 1:1 sex ratio ($P = 0.25$; $\chi^2 = 0.294$). No hermaphrodites were found. The possibility of asynchrony between males and females was considered. Separate histograms were prepared for the male and female data. Upon visual inspection the histograms showed no clear pattern of asynchrony between the sexes. As no discernable asynchrony was apparent, further analysis was considered unnecessary. The data for both sexes were pooled and are reported here.

The clams sampled in this study ranged from 15 to 88 mm in shell length. Of the 28 clams < 25 mm sampled, only a single 15 mm female in the active stage could be distinguished, the remainder showing no gonadal activity of any kind, sex being indistinguishable.

No consistent relationship between spawning condition and size could be discerned for clams over 25 mm in length. Correlation coefficients between size and spawning condition were calculated and subjected to a *t*-test, but the results were inconclusive. Clams of all sizes occurred in the various spawning categories throughout the spawning season. Mean shell lengths varied from 44.9 to 61.6 mm among the four populations studied (Fig. 2).

Candlestick Point

Sampling began in September 1979 and it was apparent that spawning was ending at that time. While 15% of *M. arenaria* were still ripe, 65% were inactive and the remaining 20% partially spawned or spent (Fig. 3). By late November, 95% of the clams

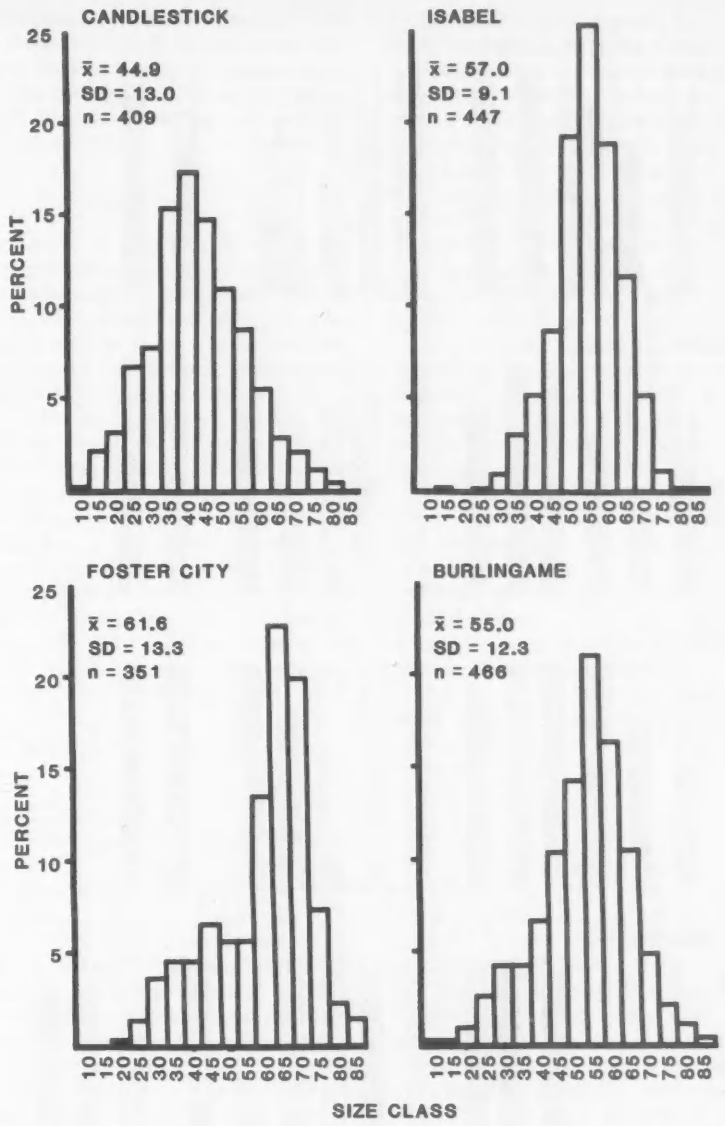

FIGURE 2. – Size-frequency histograms for the four populations studied. Size classes are (in mm) 10.0-14.9, 15.0-19.9, etc.

sampled were inactive and 5% still showed a few mature gametes which would probably have been resorbed. All individuals were inactive by the end of December 1979.

The first sign of gonadal activity appeared at the end of January 1980; by March, 82.1% of the clams sampled were active. In April, all individuals were either ripe or spawning. Peak spawning occurred

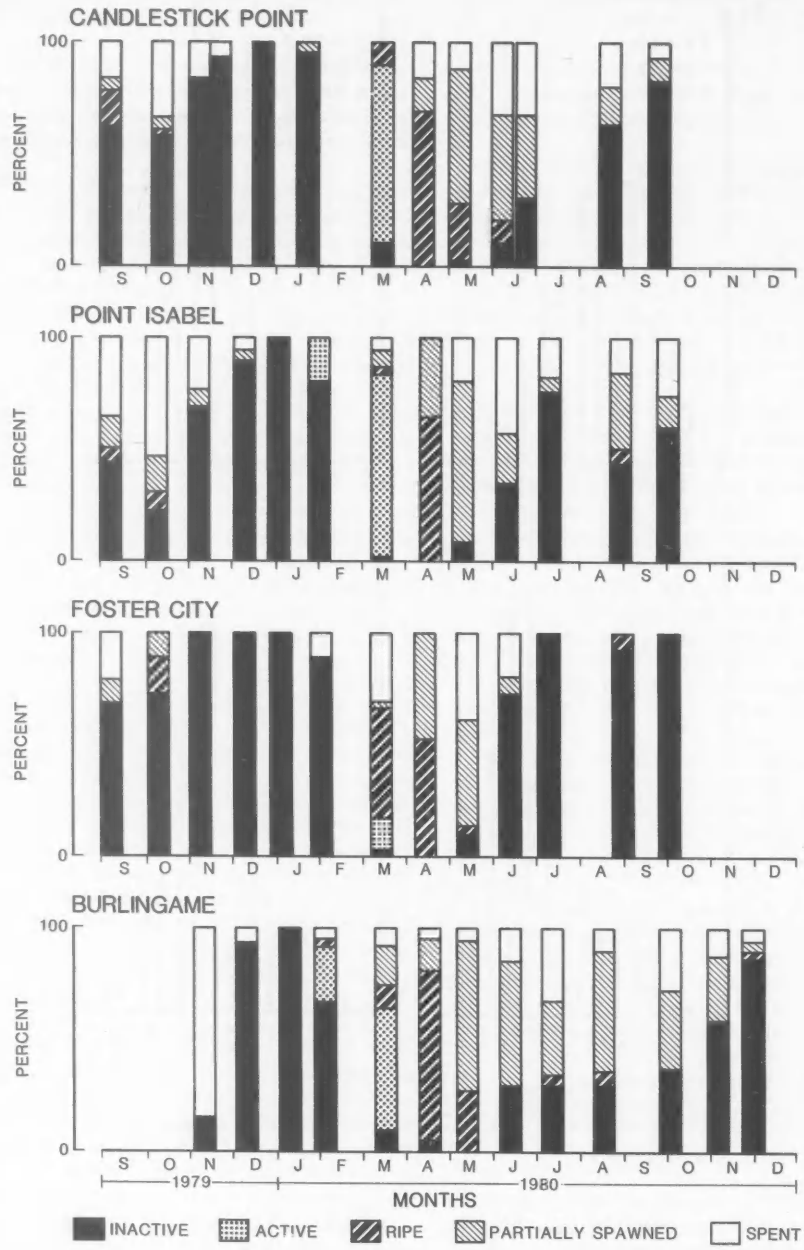

FIGURE 3.—Percentage of the clams sampled that were in each of the five categories of spawning readiness. Male and female data are pooled.

during May and June. By the end of June, the sample was roughly divided into thirds among the partially spawned, spent, and inactive stages. Some spawning could still be seen through the end of August, but by late September 85% were inactive, 10% partially spawned, and 5% spent.

Foster City

September-October 1979 marked the end of the Foster City population spawning, with most clams (70%) being inactive during this period (Fig. 3). From early November through the end of December 1979, no activity could be found. The late January 1980 sample showed a 90% active:10% spent ratio with no intermediate stages represented. It is unclear whether this indicated a rapid maturing and spawning of a few precocious individuals or an overwintering of residual gametes. By mid-March, every stage was represented, most (50%) being in the ripe stage. Peak spawning extended from the beginning of April through May, with a complete maturation-spawning season extending from late February through May. From July to late September no appreciable gonadal activity could be discerned. This lack of activity from mid- to late summer distinguished the Foster City population by its short spawning season relative to other populations (Fig. 3).

Burlingame Lagoon

Sampling of the Burlingame Lagoon population did not begin until November 1979. At the time 85% of the clams sampled were spent and only 15% were inactive (Fig. 3). This suggests a protracted spawning in 1979, similar to that which was seen in 1980. By December all but 5% were inactive and by 1 January 1980 all were inactive. Gonadal activity appeared again by the end of January 1980. Peak spawning occurred during May and June; however, spawning continued well into September and October with a full 30% of the clams of each sample being in the partially spawned stage. The Burlingame Lagoon population had the longest spawning season of the populations examined.

Point Isabel

Sampling of the Point Isabel population began in September 1979. The September and October samples still contained ripe individuals (< 10%), but most of the clams sampled were spent or inactive. By November, 70% of the clams sampled were inactive and by the end of December all were inactive (Fig. 3). The 1979 spawning season had ended for the Point Isabel population by early November.

Gonadal activity had resumed by late January. By March, 80% of the clams sampled were active. Only ripe and partially spawned individuals could be found in mid-April, and by May inactive individuals were being found (10%). Peak spawning occurred during May. Spawning continued through June and by July almost 80% were inactive and 20% partially spawned or spent. Spawning appeared to be over; however, the August sample contained almost 35% partially spawned and 5% ripe individuals. It is tempting to suggest a possible second spawning in August, but the May and June samples lacked active or ripe individuals, which suggest the August observation be attributed to sampling error. Spawning was still occurring in late September, as 15% were still in the partially spawned stage. At this time, however, 60% were inactive and 25% spent.

The four study sites showed similar trends (Fig. 4) in temperature and salinity. Temperatures fell from November through mid-January and rose from mid-January through the beginning of April and then stabilized. Temperature then climbed again from mid-May through July. The July-September temperatures were steadier at the Foster City and Burlingame sites than at Point Isabel or Candlestick Point, where they dropped markedly during this period. Salinity followed a similar trend, falling during the late winter months, and rising during spring and summer (Fig. 4). Salinity ranged from 8 to 33 ppt and temperature from 12° to 23°C.

DISCUSSION

The spawning cycle of *M. arenaria* in San Francisco Bay in 1980 was an extended one. Gametogenesis had begun by late January for three of the four populations sampled (Candlestick Point, Burlingame Lagoon, and Point Isabel), and by mid-March all five stages of gonadal development were represented in the Burlingame Lagoon, Point Isabel, and Foster City populations. Spawning had begun at all four sites by April; over 20% of the individuals from each sample were in the partially spawned or spent stages. The number of clams in these spawning stages reached a maximum during May and June 1980. Spawning continued through September and October and then ceased.

Only a single clam < 25 mm in length was found to have active gonads. This suggests that 25 mm might be generally recognized as the size at first reproduction for San Francisco Bay *M. arenaria*.

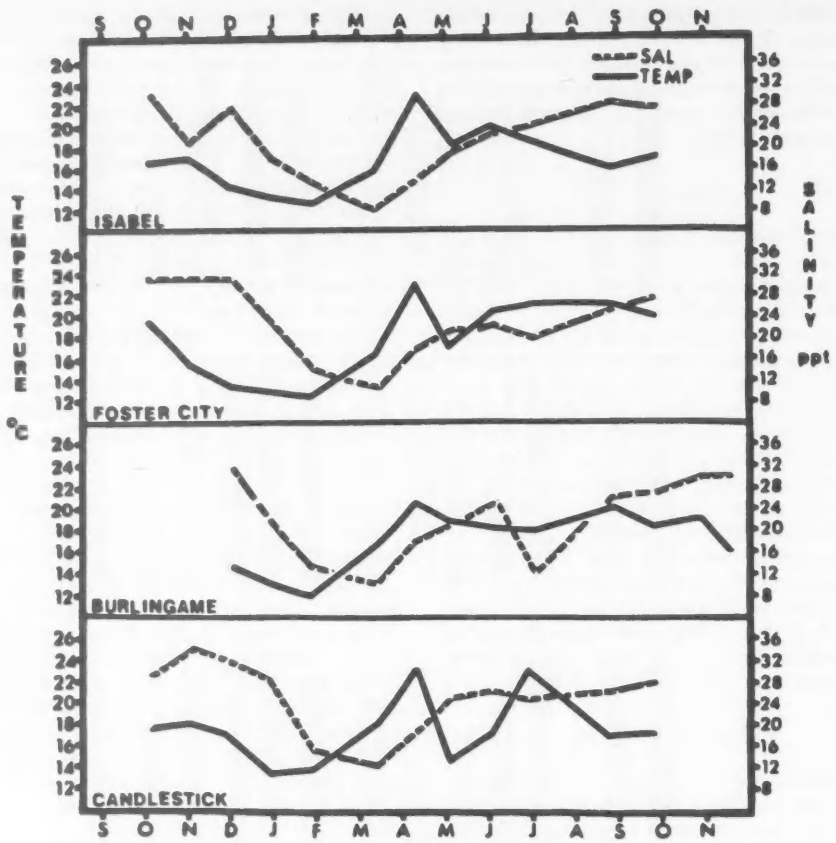

FIGURE 4.—Temperature and salinity variations during the collection period for the four collection sites, 1979 and 1980.

Although no growth or age measurements were performed in this study, the 25 mm shell length indicating a lower limit to sexual maturity corresponds to the east coast *M. arenaria* found to be late in their first year (Brousseau 1979).

Of the 313 clams that were indistinguishable as to sex, only 28 were < 25 mm in length, therefore we cannot attribute this lack of discernable sex to immaturity. Furthermore, clams of indeterminate sex were seen only during the fall and winter months (September-March) when most clams were found to be in the inactive stage. During the period of March-September or spring-fall when the active, ripe, partially spawned, and spent stages were well represented, all clams could easily be determined to be male or female. The difference between inactive male and female gonads is obvious and was seen in many clams, yet many clams which were larger than 25 mm in length and should have been sexually mature showed no signs of sexually distinguishable tissue at all. No evidence of even small oocytes or atypical spermatogenesis was seen in these clams. For the sake of simplicity, these clams were placed in the inactive stage. Perhaps this condition was a kind of "gonadal exhaustion" due to the prolonged spawning period.

The four study populations were dominated by clams ranging from 40 to 75 mm in length (Fig. 2). This size range corresponds to the 1.5 to 4.0 year classes determined by Brousseau (1979) for *M. arenaria* from Gloucester, MA. While total correspondence in growth rates between Massachusetts

and San Francisco Bay populations cannot be assumed, the age classes can be used as a first estimate of approximate age with size.

Studies of the spawning cycle of soft-shell clams from the east and west coasts of the United States reveal both similarities and differences in spawning pattern. Spawning on both coasts begins in early spring as the water warms from the lower winter temperatures. The majority of east coast populations studied show two separate spawnings each year, while populations studied on the west coast show a single more protracted spawning. Differences in the length of spawning and the number of separate spawning episodes are probably partially related to the phenology of water temperature change and the difference in the range of water temperatures that occur on either coast.

Mya arenaria in San Francisco Bay, studied during the 1979-80 season, began ripening earlier than *M. arenaria* of the New England region studied previously. Ropes and Stickney (1965) encountered active clams in eastern Maine by late January; however, ripe clams were not discovered until mid-May, and at that time none appeared to have spawned. Clams from their Booth Bay Harbor samples showed the earliest ripening, which was in April and May; by September spawning was over.

Brousseau (1978) reported a biannual cycle of spawning for *M. arenaria* from Cape Ann, MA. The first spawning at Cape Ann occurred as early as that in San Francisco Bay (March); however, it was of short duration, being over by April. A separate second spawning took place during June through July. Brousseau's figures indicate water temperatures began to rise from a low of 1°C around Cape Ann as early as mid-February, but did not rise above 10°C before May. It is possible that the increase in temperature triggered an early spawning, but the continuing, relatively cold temperature prevented an adequate build-up of mature gametes to sustain a prolonged spawning. Once spawning had taken place, the clams may have had to undergo another period of gametogenesis prior to a second spawning. Brousseau (1978, page 159) stated, "The presence of cytolyzed unspawned gametes in the summer samples suggested that the same individuals had also been ripe earlier in the year. Thus the observed spawning pattern was due to repeated spawning by the same individuals rather than asynchronous spawning of individuals within the population."

Pfitzenmeyer (1962) also reported two annual periods of spawning in *M. arenaria* at Solomons, MD. He noted that "The first umbone larvae of the year usually were found in May after the surface waters rise above 15°C or a mean temperature of 16.7°C." Salinities which remained constant throughout the spring remained near 10 ppt. This corresponds to the March temperature-salinity patterns in San Francisco Bay. During March, San Francisco clams were just beginning to spawn. Pfitzenmeyer also noted the disappearance of larvae from the Maryland waters as the temperature rose above a mean of 21.4°C. The larvae did not reappear until temperatures had fallen below this point. He concluded an optimal temperature range exists during which spawning may occur. In San Francisco Bay, temperatures rose to or above 21°C only in the following instances: Foster City–11 April - 23°C, 2 July - 21°C, 25 August - 21°C; Candlestick Point–9 April - 23°C, 30 June - 23°C; Point Isabel–10 April - 23°C (Fig. 4).

Porter (1974) noted a single yearly spawning from late May to early September among *M. arenaria* from Skagit Bay, WA. This is a shorter spawning season than seen among San Francisco Bay *M. arenaria* and may be a result of lower temperatures (4.8°-15.7°C) encountered in Washington.

Simel[5] reported a single spawning from late March through April for soft-shell clams from Humboldt Bay, CA. Generally, this more northerly part of California has a cooler climate than the San Francisco Bay area. Simel indicated that the later stages of gametogenesis corresponded with a peak in the phytoplankton abundance.

Studies of the spawning cycles of *M. arenaria* from the east and west coasts of the United States suggests a pattern of spawning behavior. Spawning begins as the water temperature rises in the spring. Pfitzenmeyer's (1962) work suggests *M. arenaria*'s optimal spawning range falls between 15° and 21°C. Differences between the spawning cycle of *M. arenaria* from San Francisco Bay and that of *M. arenaria* from New England, Canada, Washington, and northern California may be explained as the logical result of the different seasonal warming patterns and extremes encountered in the different areas. San Francisco Bay does not cool to the same temperatures as the other areas and has a much longer period of moderate water temperatures, extending from late March through summer and into September and October. Consequently, *M. arenaria*'s spawning season is equally protracted in San Francisco Bay.

[5]N. Simel, Humboldt State University, Arcata, CA 94542, pers. commun. 1982.

ACKNOWLEDGMENTS

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RECRUITMENT PATTERNS IN YOUNG FRENCH GRUNTS, *HAEMULON FLAVOLINEATUM* (FAMILY HAEMULIDAE), AT ST. CROIX, VIRGIN ISLANDS[1]

W. N. McFarland,[2] E. B. Brothers,[3] J. C. Ogden,[4] M. J. Shulman,[5]
E. L. Bermingham,[6] and N. M. Kotchian-Prentiss[7]

ABSTRACT

During 1979 and 1980 the settlement of postlarval grunts (mostly French grunts, *Haemulon flavolineatum*) from the plankton to inshore areas in Tague Bay, St. Croix, Virgin Islands, was monitored. Settlement occurred at all times of the year, but showed two distinct maxima during May-June and October-November. Summer settlement rates were approximately one-third the peak rates, whereas winter settlement rates were low but always present. A dominant, semilunar periodicity in the settlement of the postlarvae was clearly present, but smaller interspersed weekly peaks occurred. Calculation of the fertilization dates of recently settled postlarval grunts, derived from otolith ages, also established a dominant 15-day periodicity, but again interspersed with smaller weekly fertilization peaks. The phase of settlement and fertilization is most strongly associated with the quarter moons and/or intermediate daily excursions of the tides; the smaller weekly peaks are more closely associated with new and full moons. The pelagic existence of French grunts is about 15 days, suggesting that fertilizations that lead to successful recruitment to inshore areas precede settlement by 15 days. Two hypotheses – semilunar shifts in spawning versus a more constant daily rate of reproduction – are discussed as possible explanations of the dominant semilunar rhythm observed in the settlement patterns.

Community structure is primarily determined by predation, competition, environment, and patterns of reproduction and recruitment (Ricklefs 1979). In most marine fishes the larval stages are planktonic, a circumstance especially true for tropical reef fishes (Breder and Rosen 1966; Sale 1980; Thresher 1984). In general, larger reef species produce numerous but relatively small eggs, which at spawning are dispersed into the plankton; whereas smaller reef species produce fewer but larger demersal eggs, which are guarded until hatching when the larvae also "escape" into the offshore plankton community (Johannes 1978; Barlow 1981). The potential significance of this widespread reproductive strategy to affect coral reef fish assemblage structure is widely recognized (see Helfman 1978 and Sale 1980 for reviews). Most ecologists have assumed that planktonic larval fishes provide an extensive reservoir of potential recruits that settle to the reef whenever space becomes available (Sale 1977, 1978; Dale 1978; Smith 1978). Virtually all recent studies, however, emphasize that we know little of the ecology of larval fishes at sea and of their patterns of recruitment to benthic juvenile habitats (McFarland in press; McFarland and Ogden in press). Until more quantitative information on the early life history of a variety of species of reef fishes is available, models that "explain" fish community structure remain, at best, first approximations. Here we describe spatial and temporal patterns of recruitment in the French grunt, *Haemulon flavolineatum*, a dominant western Atlantic tropical reef species.

MATERIALS AND METHODS

Recently settled postlarval French grunts and white grunts, *H. plumieri*, standard length (SL) ca. 8.5 mm, are commonly observed in schools over grass beds or associating with coral clumps and gorgonians in Tague Bay, St. Croix, VI. Single individuals and larger aggregations associate with structure and/or intermix with schools of mysids (McFarland and Kotchian 1982). There is little difficulty in recognizing and counting these very small grunts in the field because they lack the body colora-

[1]Contribution No. 70 of the West Indies Laboratory.
[2]Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, NY 14853.
[3]Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, NY 14853; present address: 3 Sunset West, Ithaca, NY 14850.
[4]West Indies Laboratory, Fairleigh Dickinson University, Christiansted, St. Croix, VI 00820.
[5]Department of Zoology, University of Washington, Seattle, WA 98195.
[6]Department of Biology, University of Massachusetts, Boston, MA 02125.
[7]Department of Zoology, University of Maine, Orono, ME 04473.

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tion patterns of slightly larger postlarvae (see table 1 in McFarland and Kotchian 1982). Postlarval grunts, however, cannot be identified by sight at the species level. We will refer to these smallest postlarvae as PL-1 grunts. These recently settled postlarvae are diurnal plankton feeders (McFarland 1980) as, presumably, is the preceding pelagic larval stage. Although the postlarvae show strong social tendencies to school during daytime, they are solitary at night (Helfman et al. 1982); the same pattern is found in older juveniles and adults (Ogden and Zieman 1977). The typical stereotyped twilight migrations of older juvenile and adult grunts (Hobson 1968; Ogden and Ehrlich 1977; McFarland et al. 1979), however, are not present, nor are the agonistic behaviors typical of all later stages (McFarland and Hillis 1982).

During collateral studies on the population dynamics of grunts, on agonistic behavior in juveniles (McFarland and Hillis 1982), and age determinations of grunts (Brothers and McFarland 1981), we noted that recently settled PL-1's appeared in pulses. To investigate this periodicity, an extensive area of bottom in Tague Bay and a series of shallower discrete reef sites were censused repeatedly for PL-1's. In addition, subsamples of PL-1's were collected throughout the census period for size and age determinations.

Tague Bay Census Measurements

Sixteen flagged iron stakes were set 10 m apart along the bottom of Tague Bay parallel to the bay's barrier reef at a depth of ca. 5m. The bottom was characterized by sandhills produced by the burrowing activity of thalassinid shrimps, with stands of the seagrasses *Thalassia testudinum*, *Syringodium filiforme*, and *Halodole wrightii* between the mounds. Censuses of the total number of postlarvae were made using scuba, recording the numbers of grunts encountered along a 5 m wide transect. The census included all postlarval grunts observed over an area of 800 m^2 of bay bottom. Because almost all juvenile grunts in the immediate vicinity were French grunts, we presume the census data mostly represent this species. Of 85 PL-1's collected on this site, all were identified as French grunts. The census began on 25 February 1979, and was continued at variable intervals through 31 August 1980. Although numbers of older grunts were also recorded, here we report only the numbers of the smaller and youngest postlarvae (mean SL = 8.5 mm). This census is hereafter referred to as the "sandhill" site.

Reef Census Measurements

A series of 20 individual sites in a shallow sandy area (1-3 m depth) along a 200 m stretch of the Tague Bay barrier backreef were monitored for postlarval settlement. The sites varied somewhat in size and structure, but were composed of small clumps of *Montastrea annularis* and/or *Porites porites*. Sixteen of the sites were in depths of 1 to 2 m; four were in 2 to 3 m depth. Reef areas varied from 0.1 to 8 m^2; vertical relief from 20 cm to 1.5 m. Daily censuses were obtained as often as possible from 25 April 1980 through 25 May 1981. The census schedule was intensified especially from 6 May through 27 December 1980 (172 censuses over 236 d). Counts on each site on each census day included the total numbers of PL-1's, older postlarvae, juvenile grunts (see McFarland and Kotchian 1982), damselfishes (all species lumped), and the common sea urchin, *Diadema antillarum*, within the spines of which the middle-sized juveniles often seek refuge (see Helfman et al. 1982). In this reef area, which is surrounded by coral sand and lacks seagrass beds, juvenile white grunts were never encountered, only French grunts. We conclude therefore that recruits were all French grunts.

Reproductive Activity and Aging of French Grunts

Spawning in grunts has not been observed or reported in the literature (Breder and Rosen 1966; Hobson 1968; Johannes 1978; Lobel 1978; our personal observations and field observations of P. Colin and of E. S. Hobson). An indirect method was used to provide information on whether grunts spawned in some periodic manner, as so many reef fishes do (Johannes 1978; Lobel 1978; Colin 1982).

The age of French grunts can be established in days, for example, by counting the number of microstructural growth increments laid down in the lapillus (Brothers and McFarland 1981). The method is especially useful for aging the younger life history stages (< 100 d). By ascertaining the actual age of an individual grunt in days, it becomes possible to establish the specific date on which it was spawned. The method requires a correction, however, because the first "daily" growth increment deposited in the otolith does not coincide with fertilization of the egg. Our best "estimate" for the age at formation of the first distinct increment in the otoliths of French grunts is the third day after fertilization (for details see Brothers and McFarland 1981; this revised estimate is based on laboratory-reared porkfish, the con-

familial *Anisotremus virginicus*, of known age, supplied by Martin Moe). Thus, to each "otolith age" (= total increments counted) 2 d were added to establish the "absolute" daily age of an individual fish.

This method was applied to postlarval French grunts, collected throughout the year in the vicinity of the 20 discrete census sites. On most census days individual PL-1's were collected with a fine mesh net and fixed and preserved in 95% ethanol. Each postlarva was measured (SL) and the otoliths were removed and placed in immersion oil. The number of growth increments was counted and corrected (+ 2 d) to the actual date of fertilization.

Tides

A tidal gauge (NOAA, Ocean Survey #9751224) operates at the West Indies Laboratory dock, about 0.5 km from our Tague Bay study site. Hourly tidal heights for the year 1980 were obtained from NOAA. Missing, due to malfunction of the gauge, are records from 26 June to 9 September 1980. These missing values were approximated from calculated tidal data for San Juan, Puerto Rico. The phase of the tides in Puerto Rico matched closely the tides at Tague Bay (comparisons of dates before and after the missing records), but the actual excursion of the tides was less at St. Croix than calculated for Puerto Rico.

RESULTS

Tague Bay Sandhill Study Site

During 1979, 27 censuses were executed during 300 possible days of sampling (25 February to 21 December). The mean interval between censuses was 11.2 d ± 6.6 (1 SD), the intervals ranging from 4 to 23 d. Five population peaks were recorded, with the number of PL-1's counted between peaks often declining to < 100 individuals. The 1979 census clearly indicated that settlement was represented by a series of pulses, but the sampling intervals were too long to resolve periodicities of much less than 1 mo. Therefore, in 1980 the sampling resolution was improved by increasing the number of censuses to 47 over a possible 325 sampling days (6 February to 26 December 1980); mean sampling interval was 7.0 d ± 7.7, the shortest interval being 1 d and the longest interval 49 d (i.e., the first interval). Eleven peaks, of which 8 are distinct, establish that the postlarvae settle in pulses, with the population numbers on the bay bottom often decreasing to 0 between pulses (Fig. 1). Although the pulses in population numbers

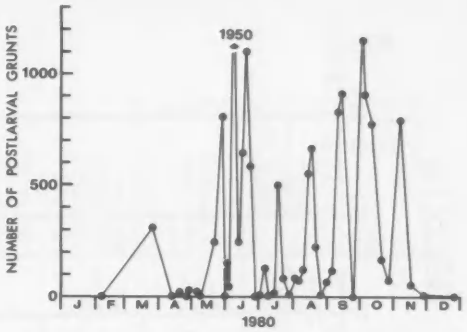

FIGURE 1. – Numbers of recently settled postlarval grunts observed over 800 m^2 of bottom on the sandhill site area of Tague Bay, St. Croix, V.I.

are suggestive of a semilunar periodicity, the peaks do not coincide more closely with either quarter moons or with the new and full moons than do the population declines.

Individual Barrier Reef Study Sites

The mean sampling interval on the 20 individual census sites from 6 May to 27 December 1980 (possible 236 sampling days) was 1.37 d ± 0.7 (1 SD). This shorter sampling interval vividly reveals the periodicity in the appearance of PL-1's on the sites (Fig. 2). Coincidence between these peaks and the peaks for the sandhill study sites is quite good (compare Figures 1 and 2) and indicates that the timing of the settlement of PL-1's is general over the entire area. Also, as in the sandhill area, the numbers of PL-1's declined to 0 between most pulses. Furthermore, the pooled data for the 20 sites indicate a bimodal seasonal influx of PL-1's, one in late spring and a second increase in fall, as seen also in the sandhill study site (compare Figures. 1 and 2). The summer settlement pulses involved about one-third the number of individuals associated with the bimodal peaks. Winter settlement was very low; only small numbers of PL-1's were observed during January and February 1981.

Age and Reproductive Activity

A total of 2,353 postlarvae from 141 collections spread over 391 d were captured between 20 February 1980 and 16 March 1981 (Fig. 3). From each of these 141 samples 15 PL-1's were measured and aged, or fewer if the collected samples contained

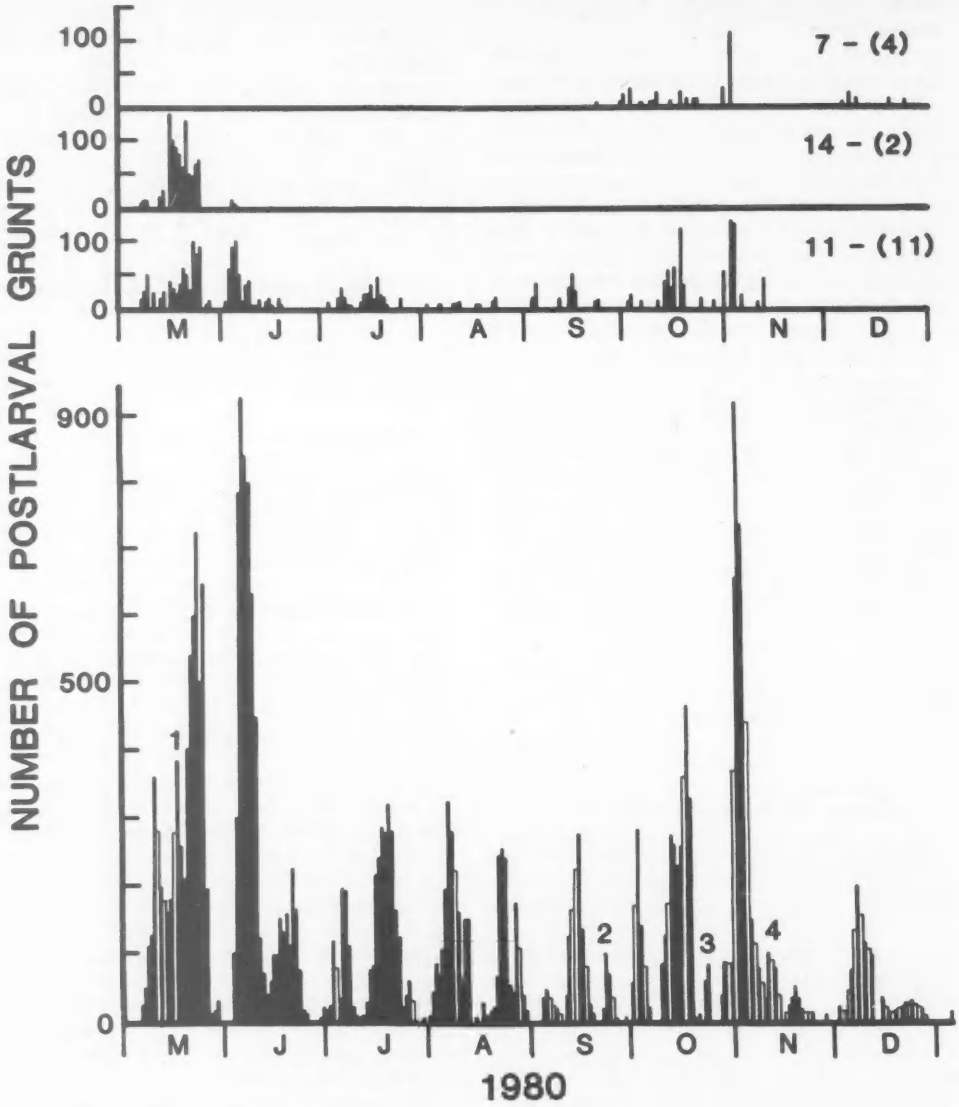

FIGURE 2.—Numbers of recently settled postlarval grunts observed on the individual census sites located in the shallows along the backreef of Tague Bay barrier reef. The three upper graphs represent the recruitment of PL-1's to specific sites 7, 11, and 14. Numbers in parentheses to the right of the hyphens indicate on how many sites a similar seasonal pattern of settlement was observed. Three of the 20 census sites were like 7 or 14, but also recruited grunts in summer (not shown). The lower graph represents the pooled data from all 20 sites. Values for census gaps have been estimated by calculating running averages (open bars). Numbers indicate the weaker but definitive weekly influxes of postlarvae. Additional weekly peaks probably occur but are less certain. Note the bimodal seasonal increase in recruitment during May-June and October-November: This coincides with the modal and bimodal peaks in gonadal development of several Caribbean reef species (Munro et al. 1973).

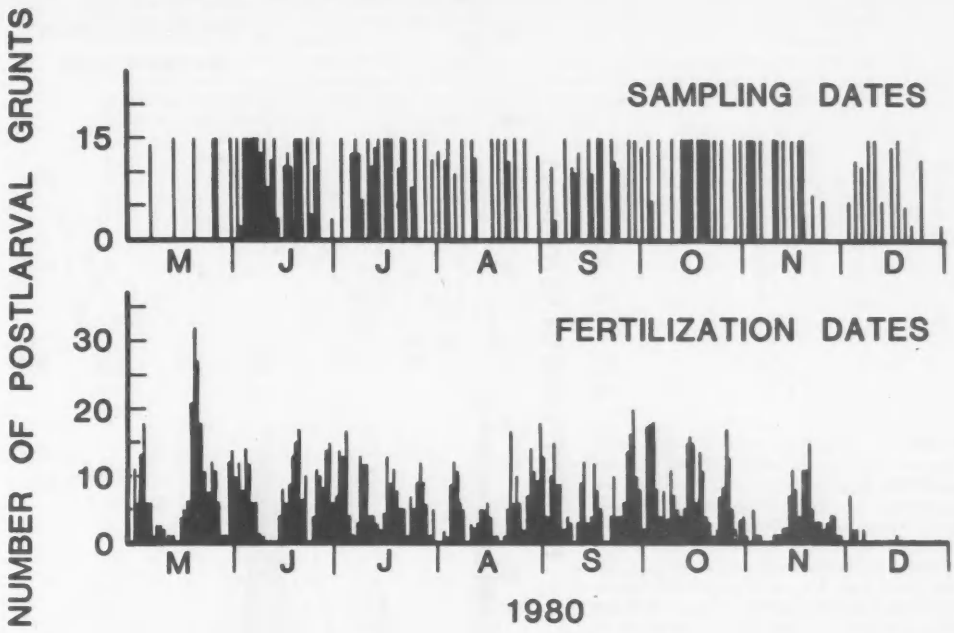

FIGURE 3. – Relationship of fertilization dates of recently settled postlarval grunts to time of the year. Upper graph represents the dates and the numbers of postlarvae collected for aging from the backreef of Tague Bay barrier reef. Lower graph represents the frequencies for back-calculated dates of fertilization of the collected samples in the upper graph.

fewer postlarvae (Fig. 3). The actual day of fertilization for each of these 1,478 French grunts indicates that recently settled individuals were spawned with a consistent periodicity (Fig. 3) that is similar to the settlement periodicity (Fig. 2). These derived spawning data suggest, however, the presence of a more pronounced short cycle.

Periodic Analysis, Times of Settlement and Reproductive Activity, and Patterns of Settlement

Periodic Analysis

To evaluate the periodicity of postlarval settlement and of fertilization times of recently recruited French grunts (Figs. 2, 3), we used a Rayleigh-test (see Batschelet 1965). The method involves a Fourier transform of sequential data (see McFarland and Kotchian 1982 for details). A data set is first sequentially summed for a specified period, and these pooled data are used to evaluate the degree of deviation from a nonperiodic random distribution. By comparing dimensions of the mean vectors obtained for different specified periods, the most dominant period is usually revealed (Fig. 4).

Analysis of the 1980 settlement and fertilization data reveals that a rhythm with a period of about 15 d dominates (Table 1). Examination of the census and fertilization data (Figs. 2, 3) indicates that weak secondary appearances of PL-1's and different fertilization dates may occur. Indeed, their presence (e.g., 4 peaks in Fig. 2) hints at a weekly rhythm superimposed on the semilunar periodicity. It is difficult to assess this possibility with periodic analysis, however, because a natural harmonic of the dominant 15-d rhythm can occur at about 7.5 d, even if a weekly rhythm does not exist (Fig. 4).

With less mathematical elegance the periodicity in the data sets can be estimated by averaging intervals between peaks. Both the 1980 census data for the 20 discrete study sites (Fig. 2) and the fertilization date data (Fig. 3) provide similar estimates of about 13.9 d and 15.1 d (Table 2), which do not differ significantly from the mean semilunar period of 14.64 d that actually occurred. The possible presence of a weekly rhythm often interspersed between the biweekly rhythm is revealed by 5 obvious short-period pulses

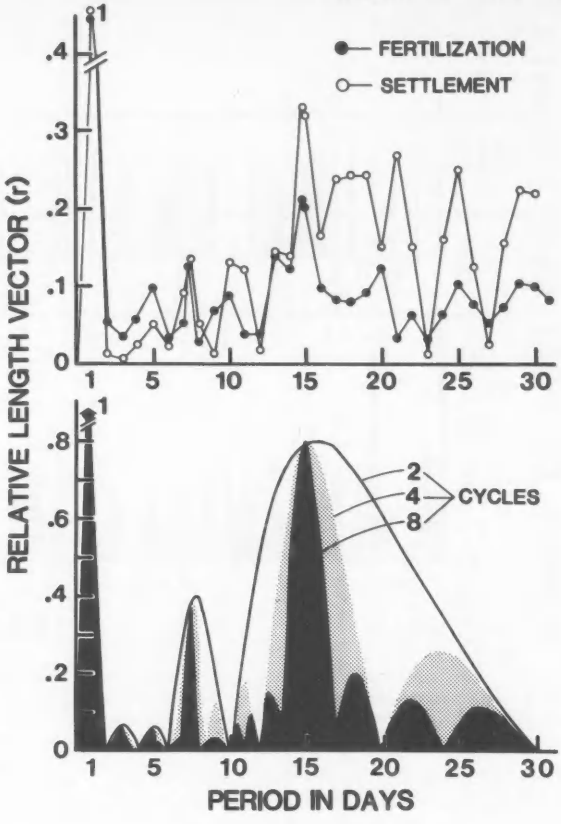

FIGURE 4.—Variation in the length of vectors derived from a circular distribution test for different periodicities in the settlement and fertilization data presented in Figures 2 and 3 (upper graph). Note that a period of about 15 d provides the largest vector value beyond a 1-d period (Rayleigh test statistic z = 28.2 for settlement and 10.8 for fertilization, where $z_{(P=0.01)}$ = 4.6). Lower graph is a plot of vector values from artificial data generated by repeating the analysis for 2, 4, and 8 cycles (artificial data were 0, 0, 0, 0, 25, 50, 75, 100, 75, 50, 25, 0, 0, 0, 0). Note how an increased number of cycles or periods narrows the peak for the dominant 15-d period and introduces more harmonics. The settlement and fertilization data (upper graph) represent 16 cycles for a period of 15 d. The height of the harmonics after 15 d probably reflects basic sampling noise and the presence of smaller weekly peaks (see Figs. 2, 3).

TABLE 1.—Dominant periods derived from a circular distribution test of the settlement and fertilization data presented in Figures 2 and 3. Significance symbols are ** = $P <$ 0.01; z values are Rayleigh test statistic (Batschelet 1965).

Type of data	Date of samples	Dominant period (days)	z value	No. days	No. cycles analyzed based on dominant period
Settlement	30 Aug.-31 Dec.	14.9	26.5**	244	16.4
	2 May-31 Aug.	15.3	19.2**	122	8.0
	30 Aug.-31 Dec.	17.0	31.6**	124	7.3
Fertilization	2 May-31 Dec.	14.8	10.7**	244	16.5
	2 May-31 Aug.	14.6	8.7**	122	8.4
	30 Aug.-31 Dec.	15.5	2.8 n.s.	124	8.0

for settlement and at least 9 short-period pulses for fertilization (Table 2).

Timing of Settlement and Fertilization

To estimate the phase of settlement and of fertilization to the lunar cycle, the delay in days from the nearest full or new moon was determined for each event (Table 2). The mean phase delay for fertilization was 5.4 d, and for settlement 7.3 d. Clearly both fertilization and settlement are more often associated with the quarter moons than they are with the full or new moons. The overall relation to the lunar cycle is revealed more clearly by matching each in-

TABLE 2.—Comparisons of fertilization and settlement dates for recently recruited postlarval French grunts with the lunar cycle and the state of the tides. F and N are full and new moons; S and N are spring and neap tides; I↑ and I↓ are rising and falling tides of intermediate amplitude between a spring and a neap tide. The peak date for settlement represents the maximum influx of postlarvae, which occurred on average 3 d before the maximum number of French grunts appeared on a site. Values are the sums from all 20 census sites. Rows are aligned so that the most likely fertilization date precedes each settlement date. Vertical lines and summed numbers for days between peaks are best estimates of weekly peaks to yield the dominant biweekly peaks (see mean values at bottom of table).

Fertilization					Settlement				
Peak date	No. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state	Peak date	Total no. PL-1's in peak	No. days between peaks	Moon phase + days	Tidal state
—	—	—	—	—	4/7	[1]18	—	F+7	I↓
—	—	—	—	—	4/22	[1]13	15	N+8	I↓
—	—	—	—	—	5/7	360	15	F+7	I↓
—	—	—	—	—	[2]5/14	383	7	N+0	S
5/4	49	—	F+4	S	5/20	723	6 13	N+6	I↓
—	—	—	—	—	[2]5/26	29	6 13	N+12	I↑
5/19	48	15	N+5	I↓	6/3	930	7	F+5	I↓
5/30	18	11	F+1	S	6/18	224	15	N+6	I↓
6/19	21	20	N+7	I↓	7/3	195	15	F+5	I↓
[2]6/28	20	9 14	F+0	S	—	—	—	—	—
7/3	34	5	F+5	I↓	7/17	317	14	N+5	I↓
[2]7/7	21	4 14	F+9	I↑	—	—	—	—	—
7/17	19	10	N+5	I↓	8/4	324	18	F+10	I↑
[2]7/25	16	8 19	F+0	S	—	—	—	—	—
8/5	18	11	F+11	I↑	8/20	255	16	N+10	I↑
[2]8/10	8	5 15	N+0	I↓	9/2	45	13	F+9	I↑
8/20	12	10	N+10	I↑	—	—	—	—	—
[2]8/30	24	10	F+5	S	9/12	226	10	N+3	N
9/3	15	4 13	F+9	S	[2]9/20	100	8	N+11	I↓
[2]9/12	17	9	N+3	I↑	—	—	— 18	—	—
9/16	18	4	N+7	I↑	9/30	280	10	F+6	S
[2]9/21	11	5 15	N+12	I↓	—	—	—	—	—
9/27	20	6	F+3	I↑	—	—	—	—	—
[2]10/2	21	6 11	F+8	I	10/15	462	15	N+7	S
10/8	15	5	N+0	I	[2]10/21	82	7 17	N+13	N
[2]10/14	19	6 12	N+6	S	10/31	917	10	F+8	I
10/25	17	6	F+2	I	[2]11/8	100	8 16	N+1	I
[2]11/2	5	11	F+10	N	11/16	50	8	N+9	I
11/19	17	8 14	N+12	N	12/5	199	19	F+13	I
[2]11/25	5	6	N+3	I	—	—	—	—	—
12/1	6	6	N+6	N	—	—	—	—	—
Mean days between peaks including weekly peaks			7.6 ± 1.4 (2 SE)				11.5 ± 1.8 (2 SE)		
Mean days between peaks excluding weekly peaks			13.9 ± 1.6 (2 SE)				15.1 ± 1.1 (2 SE)		
Mean days from F or N moon			5.5 ± 1.5 (2 SE)				7.3 ± 1.5 (2 SE)		

[1]These two peaks are from sites adjacent to the 20 study sites and were abandoned after April.
[2]The peaks for these dates approximate weekly fertilization and recruitment pulses interspersed between the biweekly peaks for recruitment (see also Fig. 6).

dividual settlement date and fertilization date to the time of full moon (Fig. 5). Several features stand out: 1) The settlement data are less noisy than the fertilization data; this is explained, in part, by the more strongly expressed weekly patterns in the fertilization data. 2) Although settlement is clearly associated with the quarter moons, it does occur during other periods of the lunar cycle as well (see also Table 2, Fig. 2). 3) Fewer PL-1's are present on the sites during full moons than during new moons.

The relation of settlement pulses to daily tidal excursions (Fig. 6) indicates that settlement was most often associated with rising or falling (intermediate) stages of the tidal cycle than with spring or neap tides. A more extensive evaluation of the results reveals that out of 22 identifiable settlement pulses, 17 occurred during intermediate tides, 3 with spring highs, and 2 during neap tides. Also, out of 26 fertilization periods, 16 occurred during intermediate tides, 7 on spring highs, and 3 during a neap tide.

If a specific state of the moon, such as the quarter moons, is the significant environmental factor that determines the timing of fertilization and/or settlement of French grunts, then the state of the tides

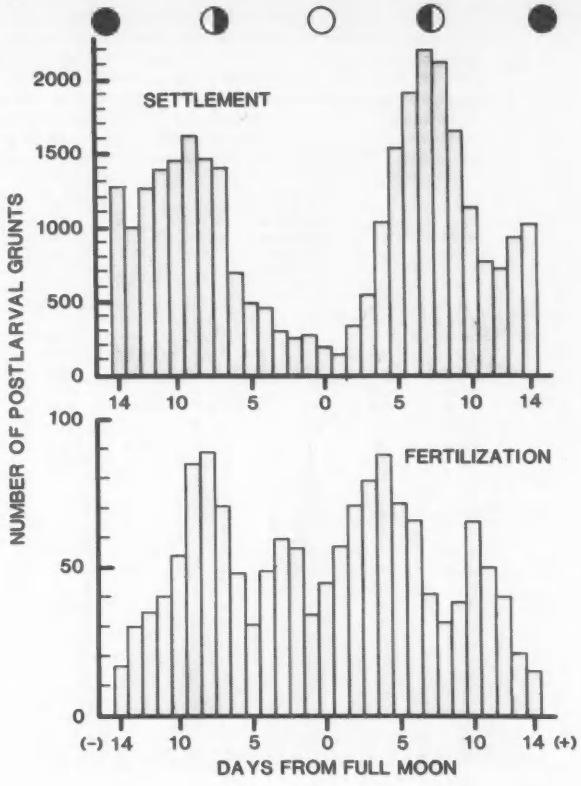

FIGURE 5.—Lunar phase relationships of settlement and fertilization dates for French grunts. Data represent the totals obtained from Figures 2 and 3 summed with reference to the days before and after full moons. The settlement data are the sum of peak numbers of PL-1's on all census sites. Actual settlement rates (maximum rate of influx) were maximal 2 to 3 d before the figured peaks. The fertilization data clearly reveal weaker weekly periods of spawning (see text for details).

should be unimportant. This condition would prevail because the tidal states (springs, neaps, intermediate conditions) change phase relative to the lunar cycle as the year progresses (Fig. 6). In contrast, if a particular state of the tide served as a primary trigger for fertilization and/or settlement then the moon's state would be unimportant. To test for the importance of tidal and lunar state the data were analyzed using a log likelihood statistic (g-test, Table 3) by grouping the 22 settlement and 26 fertilization peaks into the 9 possible combinations of tidal and lunar state (e.g., spring, neap, and intermediate tides and full, new, and quarter moons). Clearly both the lunar cycle and tidal state have significant effects on settlement and fertilization, but their interaction, although large, is nonsignificant. Because 60 to 80%

TABLE 3.—Summary of comparisons of lunar cycle and tidal state for fertilizations and settlement pulses of French grunts during 1980. Data from Table 2. Log likelihood test from Sokal and Rohlf (1981).

	g-value and associated chi-square	
Category	Settlement data	Fertilization data
Total G[1]	$36.7 > \chi^2_{.001(8)} = 26.1$	$22.5 > \chi^2_{.01(8)} = 20.1$
Moon alone[2]	$11.3 > \chi^2_{.01(2)} = 9.9$	$7.3 > \chi^2_{.05(2)} = 6.0$
Tide alone[2]	$18.0 > \chi^2_{.001(2)} = 13.8$	$10.2 > \chi^2_{.01(2)} = 9.9$
Moon-tide[3]	7.4 ns $< \chi^2_{.05(4)} = 9.5$	4.9 ns $< \chi^2_{.05(4)} = 9.5$

[1]Single classification of all categories.
[2]Single classification of moon or tidal state alone.
[3]Two-way classification, moon phase versus tidal state.

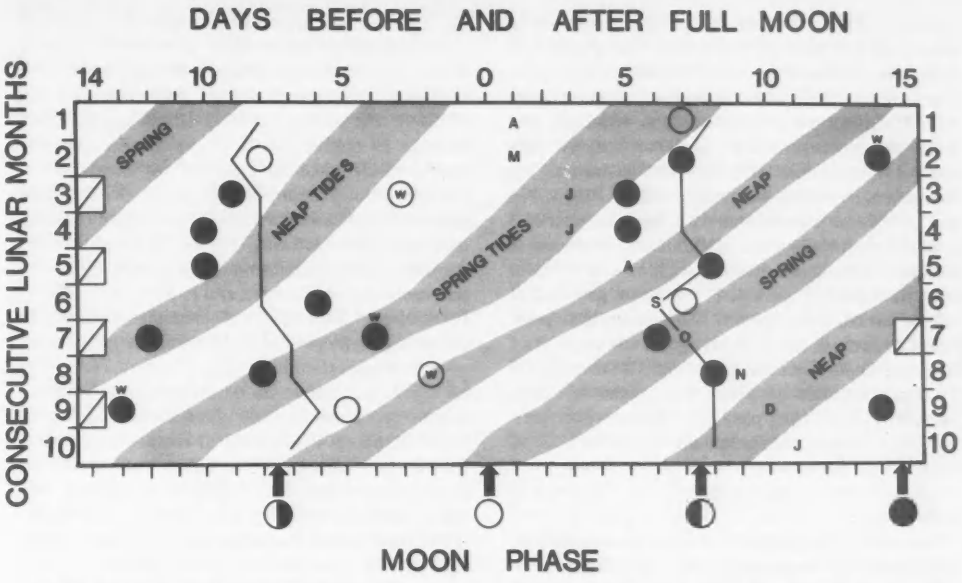

FIGURE 6. – Relation between the periodic settlement pulses of postlarval grunts during 1980, the phases of the moon, and the procession of spring and neap tides. Shaded areas represent relatively uniform series of neap or spring tides; unshaded areas are either increasing or decreasing intermediate tides (see Table 2). The sequence of days reads from left to right across each row. The first day of each calendar month is indicated by the letters, e.g., A at top = April 1980, . . . , J = January 1981. Closed circles represent the large and intermediate-sized pulses (> 100 PL-1's); open circles are settlement pulses with < 100 individuals (see Table 2). Closed and open circles with the letter w are weekly recruitment pulses interspersed between the more common biweekly peaks (see Table 2). The two abruptly changing vertical lines indicate the actual dates of the quarter moons at different times of the year, as determined from the Nautical Almanac for 1980. The mean deviations of those pulses most closely associated in each month with the quarter moons are: first quarter moon = 1.7 d ± 1.9 (SD), third quarter moon = 0.9 d ± 0.8 (SD). Maximum tidal excursions for spring tides occurred in May and June, and in October and November, as did the maximum recruitment of PL-1's to the census sites (Fig. 2, Table 2).

of the settlement pulses and fertilizations were associated with quarter moons and intermediate tides (Table 2), attempts were made to isolate the significant categories by combining the data (springs + neaps versus intermediate tides; full + new moons versus quarter moons). Nonsignificance occurred in all combinations with the exception of tides and settlement (g-test = 9.91 > $\chi^2_{.05(1)}$ = 3.84).

The relationship between fertilization and settlement of French grunts and the state of the tides and lunar cycle is obviously complex and difficult to unravel without ambiguity. Larger sample sizes (data over several years) would help, but perhaps more important would be specific data on current regimes at actual spawning sites and in the general vicinity of settlement sites. The highly significant but independent effects of moon and tidal state likely point at the importance of favorable currents to successful larval recruitment.

Settlement of Postlarvae in Space and Time

From May through December 1980, when the census frequency was high, there were 16 consecutive quarter-moon periods. On the 20 census sites, therefore, a total of 320 separate pulses (16 × 20) could have been observed if settlement did occur during the quarter moons. During this period 161 pulses were actually observed on the 20 sites during quarter moons. When the number of PL-1's settling was high, most sites recruited fish (90% for May-June, 75% for October-November). In winter, when the number of fish settling was low, recruitment nevertheless occurred on at least 4 or more sites during the quarter moons.

The periodic appearance of PL-1's on 11 of the 20 sites was virtually continuous at each quarter moon, and similar in general pattern to that depicted by the pooled data (e.g., site 11, Fig. 2). On 4 sites,

however, PL-1's settled in spring-summer or in summer-fall. These differences in the pattern of settlement between the census sites are highly significant ($P << 0.001$, "distribution-free" nonparametric test; Hollander and Wolfe 1973, p. 139-146). The patterns were so consistent, however, that we were soon able to predict with considerable success not only when, but which sites would attract PL-1's. We can provide no correlations with depth or area of a site, nor with the species of corals and other major residents (fishes, sea urchins, etc.), as to why some sites consistently "attracted" postlarval grunts and others varied, even though it is known that postlarval settlement can be partly governed by priority effects on reefs (Shulman et al. 1983). To understand the characteristics of a site that make it highly "attractive" to settling postlarval grunts will require sophisticated field manipulations.

DISCUSSION

The most conspicuous features concerning the recruitment of French grunts from the plankton are the rhythms in settlement and fertilization dates (Figs. 2-4). The continuing and short 15-d periods of these rhythms over an entire year contrast with other coral reef fishes where settlement, although rhythmic, is concentrated mostly around a particular period of the year (Williams and Sale 1981). Settlement in reef fishes is often episodic; it may show a lunar periodicity (Johannes 1978), it may be monthly but not coupled to a particular phase of the moon (Williams 1983 – mixed guild of pomacentrids), or a rhythm may not be conspicuous (Victor 1982, 1983 – *Thalassoma bifasciatum*).

The short period between fertilization and settlement implies that pelagic existence in French grunts is of short duration (about 2 wk; Brothers and McFarland 1981). To estimate the days spent in the plankton, the average age for the smallest 100 PL-1's was calculated from the sample of 1,478 fish that were used to estimate the actual day of fertilization [mean age = 15.7 d ± 2.1 (SD), range = 13-20; mean length (SL mm) = 6.9 ± 0.67 (SD), range = 5.9-8.5]. If each of these fish had settled from the plankton over the previous day, then pelagic existence (about 15 d) agrees with the periodicity of fertilization and settlement (Table 3, Fig. 4). In contrast, the pelagic existence of most other coral reef fishes investigated exceeds 15 d (Randall 1961; Johannes 1978; Sale 1980; Barlow 1981). This has been verified by results for age at settlement as determined from otoliths (Victor 1982, 1983; Brothers et al. 1983; Brothers and Thresher in press and unpublished; Thresher and Brothers in press). Most of these fishes settled at various ages: *Thalassoma bifasciatum*, 40-72 d; *Paragobiodon melanosoma*, 39-47 d; *Gobiodon* sp., 27-38 d; several unidentified scarids, 34-58 d; and labrids, 21-56 d. Direct aging of new recruits or otolith counts to presumed settlement marks rarely yield ages as low as found for the French grunt. Examples of species with pelagic phases of 20 d or less include the angel fish, *Holacanthus paru* (Brothers and Thresher in press); several damselfishes, *Glyphidodontops rollandi*, *Pomacentrus amboinensis*, *P. popei*, and *P. wardii*; the blenny *Petroscirtes mitratus*; the nemipterid *Scolopsis dubiosus* (Brothers et al. 1983); and the goby *Gobiosoma prochilos* (Brothers, unpubl. data). These may be exceptional cases; all or at least most of these species represent families characterized by having larval durations moderately to considerably longer than found in grunts. At the family level, therefore, only the haemulids, and perhaps the lutjanids, provide evidence of a short pelagic existence. In support of this conclusion is the lack of haemulids or lutjanids amongst the larval fishes collected offshore throughout the Caribbean (Richards 1981, footnote 8). Are haemulids programmed for short larval lives? We cannot be sure, but out of the 1,478 recently settled French grunts we have aged, not one exceeded 20 d from fertilization. Such a developmental process would be crucial in their survival; if they do not drift over suitable substrates on which to settle after 2 wk, they would perish offshore.

Our observations of a strong semilunar periodicity in French grunt recruitment, coupled with what seems to be a relatively fixed or invariant larval duration, could be the result of a number of different combinations of spawning and survivorship. Because we can only determine fertilization dates for individuals that have successfully recruited, we cannot be certain whether the apparent periodicity in spawning is an accurate representation of the temporal pattern of grunt reproduction. At the other extreme, it may be the result of relatively continuous spawning activity, the products of which survive differentially with respect to semilunar environmental variables.

Surprisingly, for such common fishes, little is known about spawning in haemulids. They produce pelagic eggs and larvae (Breder and Rosen 1966; Saksena and Richards 1975). Recently, paired spawning has been described for *Hapalogenys mucronatus* in aquaria (Suzuki et al. 1983). On six

[8]W. Richards, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149-1099, pers. commun. October 1980.

specific attempts to validate spawning in French grunts in the sea at St. Croix, two of us (McFarland and Shulman) failed to observe reproductive activity during dusk, but we did observe what appeared to be sporadic spawning by small groups of tomtate grunts, *Haemulon aurolineatum*, within large schools of these fish. These limited data suggest that grunts, like many reef fishes, cast pelagic eggs into the water column at dusk. We emphasize, however, that there are no data about their daily spawning habits.

Two hypotheses offer explanations for the dominant semilunar periodicity of fertilization and settlement.

Hypothesis 1. Assumption: Spawning follows a semilunar rhythm with breeding peaks closely coupled to the quarter moons (and/or intermediate monthly tides). If reproductive activities in French grunts follow a semilunar cycle, and pelagic life is programmed for 15 d, then settlement should occur most often during the quarter moons and intermediate monthly tides, which it does (see Table 3, Fig. 6). This hypothesis, however, does not account for the weekly peaks in settlement and fertilization (Table 3; Figs. 2, 3, 5), which contradict the assumption of the hypothesis.

Hypothesis 2. Assumption: Spawning is relatively constant from day to day, and larval existence restricted to about 15 d. Consistent daily reproductive effort could produce a continuous pool of grunts in the plankton. As a result, only those larvae that are favored by "correct" currents that disperse them inshore around 15 d will settle, and/or successful recruitment may also depend on favorable currents dispersing the eggs at the time of reproduction. At St. Croix we suspect that current conditions are most favorable to settlement during the quarter moons and intermediate tides. The weekly peaks that are associated with full and new moons (Table 3) could represent recruitment in less favorable currents than occur around the quarter moons. These currents, nevertheless, must allow some larvae through the "filter screens" that all recruits must pass through to join a reef community (Smith 1978). The semilunar rhythm of fertilization and settlement observed in settling grunts would, under this hypothesis, be explained by semilunar rhythms in currents favorable to settlement.

The time of day when settlement occurs and, especially, the amount of darkness at night may also relate to successful settlement. Although data are scarce, some reef fishes settle from the plankton at night (e.g., acanthurids–Randall 1961; McFarland, unpubl. data). We do not have similar direct observations for French grunts, but we suspect settlement is nocturnal because the number of PL-1's remained fairly constant on most census sites throughout each day. Nocturnal settlement behaviors would temporarily remove recruits from the attack of reef piscivores, especially if accomplished during the dark of the moon. During full moons, recruits presumably would be subject to higher rates of predation by planktivores than during other phases of the moon (Hobson et al. 1981). The number of grunts settling during full moons should be low, which it is (Fig. 4). In contrast, if length of darkness is a dominant factor to successful settlement, then the highest influx of recruits should coincide with the new moons, and intermediate numbers with quarter moons, which they do not (Fig. 4). The recruitment dynamics, nevertheless, indicate higher influxes of PL-1's when some degree of darkness occurs during each night (Fig. 4). We hypothesize that recruitment is dependent primarily on favorable currents, with predation possibly acting as a secondary selective force.

Reversals in surface currents and oppositely flowing currents in the upper 30 m, which could affect the dispersal of larvae, are known to occur at St. Croix and at Puerto Rico (Gladfelter et al. 1978; Lee et al. 1978; Molinari et al. 1980). Their local patterns, however, remain unknown. Eddy formation to the west of the island of Barbados, produced by Karmen trails as the generally west-setting current passes the island, has also been postulated to retain the pelagic stages of inshore species (Emery 1972). It is reasonably well established that seasonal shifts in local current gyres in the vicinity of Hawaii favor the settlement of various species of reef fishes (Sale 1970, 1980; Johannes 1978). In addition, spawning is often synchronized to disperse eggs and larvae away from reefs and into offshore currents (Johannes 1978; Lobel 1978). But specific currents do not always trigger spawning, as Colin (1982) reported for several reef fishes at Puerto Rico. In these instances, rhythmic spawning often can be related to the lunar cycle, but significantly, some species spawn every day. Depending on the time of spawning, dispersal routes for fish eggs and larvae can vary over short-time periods because of reversals in currents.

The daily behaviors and distributions of grunts at sea are unknown. Do larval grunts passively drift with currents? Or do they seek different depths at different times of the day? Active behaviors that would utilize differences in currents have been invoked to explain the retention of pelagic larval fishes and invertebrates close to the island of Oahu (Leis 1982). Similar activities by larval French grunts

could explain their absence in collections taken offshore (Richards 1981).

We have provided substantial evidence that French grunts recently recruited from the plankton are fertilized about 15 d earlier, and that these processes most closely correlate with the quarter moons and intermediate tidal excursions. Is this a general pattern that occurs throughout the Caribbean and western Atlantic where French grunts are most abundant? Or is the lunar-tidal correlation the result of local conditions? We have no answer at present, because it requires repeating the investigation in other localities. Different current regimes and local hydrographic conditions in other regions might elicit different recruitment patterns. The much weaker weekly fertilization and settlement patterns, for example, that are associated with full and new moons (Table 3) might dominate recruitment in other locales.

There is a seeming order in the rain of young French grunts from the plankton. Over the period of this study young grunts following a semilunar timetable appeared on over half of the census sites 70% of the time (range 59 to 94%). Although we could not discern any special characteristics of these sites that attracted grunts, the sites were never preoccupied by other species. Settlement certainly did not appear to be a random phenomenon. The recurrent order in the occupation of space by settling French grunts, however, may reflect only their high abundance in the reef communities at St. Croix (Gladfelter and Gladflelter 1978). Large populations produce large numbers of offspring and this alone might swamp available sites. In this regard we stress that the census settlement sites are not main reefs, but isolates adjacent to them. Indeed, large coral domes in the census area which sustained large populations of older juvenile French grunts never sustained populations of PL-1's. Without manipulative studies of grunts on the settlement sites, however, it is impossible to ascertain to what extent recruitment is influenced by a resident population (Shulman et al. 1983). We can conclude only that the recruitment of French grunts from the plankton has high temporal and spatial predictability at St. Croix.

Fishes in the family Haemulidae represent a dominant component of the tropical reef fish community and constitute a major part of the trap fishery in western Atlantic and Caribbean waters (Dammann 1980; McFarland 1980). The findings presented in this study provide insights that are critical to the management of any fishery for grunts. For example, the relatively short larval existence in French grunts, which also occurs in white and tomtate grunts (Brothers and McFarland 1981), implies that dispersal does not occur over very long distances. Whether local populations of grunts are self-sustaining or dependent on interisland transport is unknown. Answers will require precise knowledge of spawning habits of each species of grunt, careful analysis of local and general current regimes, and, if possible, the behavior of the larvae. If local populations are self-sustaining, then overly lenient limits on the harvest of adult grunts could seriously limit recruitment. In contrast, if recruitment shows large spring and fall peaks in other species of grunts, as it does in French grunts, and the seasonality in recruitment is geographically widespread (e.g. Munro et al. 1973), then closure of a grunt fishery for a few months during periods of peak recruitment would probably assure maintenance of the local populations.

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THE HARBOR PORPOISE, *PHOCOENA PHOCOENA*, IN FISH HARBOUR, NEW BRUNSWICK, CANADA: OCCUPANCY, DISTRIBUTION, AND MOVEMENTS

DAVID E. GASKIN AND ALAN P. WATSON[1]

ABSTRACT

The distribution, movements, and relative population abundance of harbor porpoises were studied in the Fish Harbour region of New Brunswick, Canada (lat. 44°59'30"-45°01'00"N, long. 66°54'00"-66°57'00"W), from 1970 to 1978. In any given year numbers of this species were highest in the region between late July and early September. This is also the period during which surface temperatures attain a maximum (10°-12°C) and the largest herring, *Clupea harengus*, catches are usually made. During July-September the porpoise population of the inner (western) part of the study area contained 63% mothers with calves. Changes in relative population abundance were most strongly related with time of year (increasing from early July), tidal amplitude (most present when amplitude is 6.5 m or less), and wind phase (most present during onshore winds). Observation of recognizable individuals revealed consistent specific "territories" and patrolling patterns. A marked decrease in relative abundance in the latter half of the 1970s was noted. This decrease was coincident with a decline in mean midsummer surface temperature over 1974-78 of about 1°C. Unfortunately it was not possible to determine from existing data if major changes in availability of prey species also occurred in the inner Quoddy region during the same period.

Literature concerning ecology of the harbor porpoise, *Phocoena phocoena*, has been largely restricted to reports of nonquantitative or casual observations (Scheffer and Slipp 1948; Møhl-Hansen 1954; Amundin and Amundin 1974), although more recently Gaskin (1977), Prescott et al. (1981),[2] Flaherty and Stark (1982),[3] Kraus et al. (1983),[4] and Taylor and Dawson (1984) have presented information from surveys and some population estimates for limited areas of both east and west coasts of North America. A population estimate for the Copper River area of Alaska was provided by Matkin and Fay (1980). Habitat indices, relating occurrence of animals in coastal waters to various environmental factors have been given by Smith and Gaskin (1983) and Watts and Gaskin (in press), and some radiotelemetric studies of distribution and movements by Gaskin et al. (1975) and Read and Gaskin (1983, in press).

In order to gain insight into the nature of local distributions and movements of *P. phocoena* over an extended period, we selected a semi-enclosed area of limited size in southern New Brunswick, Canada. Preliminary observations had already shown that the species was common in the area, and locality (about 8 km^2 maximum) bounded approximately by lat. 44°59'30"-45°59'00"N, long. 66°54'00"-66°57'00"W on the east coast of Deer Island (Fig. 1) was easily accessible for research and relatively sheltered. We were also aided by the occurrence in the area of several recognizable porpoises with surface disfigurements, large blemishes, or distinctive pigmentation patterns visible at some distance in favorable light; several of these animals were present in successive seasons.

CHARACTERISTICS OF THE STUDY AREA (Figure 1)

Average depths range from about 8 m in Lords Cove to about 22 m in Simpson's Passage (respective maxima 20 m and 60 m) at mean low water. The region is subject to anomalistic, semidiurnal tides of

[1]Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

[2]Prescott, J. H., S. D. Kraus, P. Fiorelli, D. E. Gaskin, G. J. D. Smith, and M. Brander. 1981. Harbor porpoise (*Phocoena phocoena*): Distribution, abundance, survey methodology and preliminary notes on habitat use and threats. Final report to U.S. Department of Commerce, NOAA, National Marine Fisheries Service Contract 80-FA-d-00009, 61 p.

[3]Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound". Final report for Subcontract 80-ABA-3584, NOAA, NMFS, National Marine Laboratory, Seattle, WA, 84 p.

[4]Kraus, S. D., J. H. Prescott, and G. S. Stone. 1983. Harbor porpoise, Phocoena phocoena, in the U.S. coastal waters of the Gulf of Maine. A survey to determine seasonal distribution and abundance. A report to the National Marine Fisheries Service, Woods Hole, Massachusetts, July 1983, 15 p.

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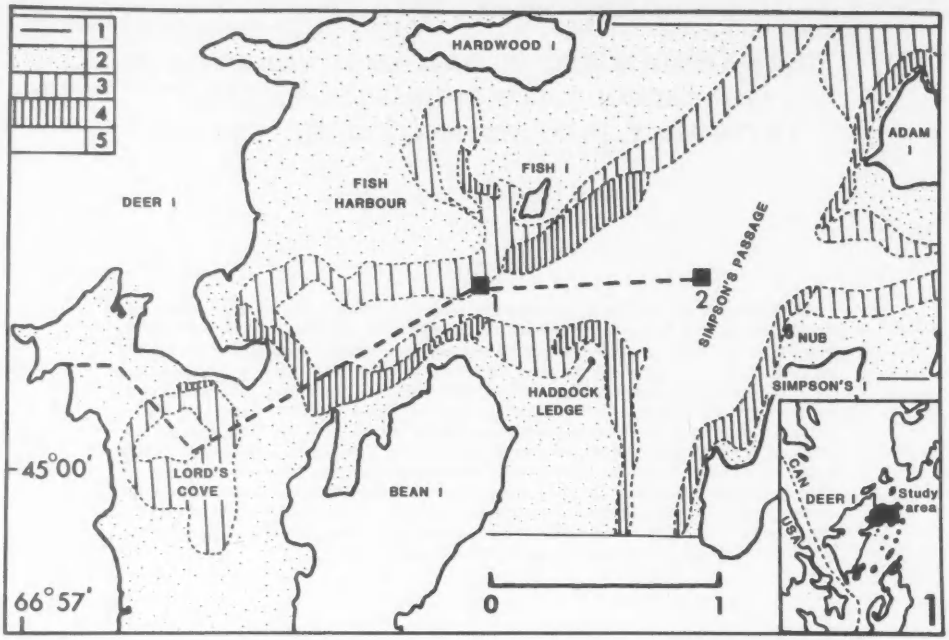

FIGURE 1.—The Fish Harbour region on the east coast of Deer Island region, New Brunswick, Canada (see inset). Legend: Straight solid lines indicate approximate limits of study area. Stipple indicates shallow shelf area (low water mark to 5 m); widely spaced vertical lines indicate areas of relatively gentle slope; narrowly spaced bars indicate steep scarps or slopes terminating in cliffs and the white areas (other than within island boundaries) are relatively deep basins and channels. Broken line shows regular track of boat with watch-stations 1 and 2. Place names are those used in the text. Scale = 1 km.

5.6-8.3 m (mean about 6.3 m) (Forrester 1960). Water turbidity is high (Secchi disk reading in July-August about 2 m). Most tidal flow from the area is by the northern end of Simpson's Passage. Salinities in the whole Quoddy region (Trites 1962) range from 29.5‰ (March-May) to 32.3‰ (September). Lower salinities in shallow inshore waters occur after heavy rain and may last for several days. While some year-to-year changes in mean surface temperature were recorded (Trites 1962, fig. 11), one of the most complete series (for 1978) provides a typical sequence of the relative changes from spring to autumn. Late May-early June surface temperatures ranged from 6.0° to 7.1°C, mid-July from 8.4° to 9.6°C, and mid-August-early September from 10° to 11.2°C. By early December the waters were 7°C again. Peak summer values of 11.3°-14.5°C were only obtained in mid-August at the head of Lords Cove in shallow water (< 5 m). At any given time surface temperatures were 0.5°-1.0°C warmer than those at 12 m despite the tidal mixing which obviously occurred. A general pattern of temperature profiles could be recognized in midsummer: The inner (western) part of Fish Harbour was vertically well-mixed throughout, but a rather steep horizontal gradient of about 1.0°C was maintained at all depths on the outer margin of this zone. In the central region (near Fish Island) the direction of water movement showed up to 90° variation at different depths at any given time of rapid tidal flow. The outer parts of Fish Harbour, and Simpson's Passage, tended to be well-mixed vertically, but were always about 0.5° cooler at the surface on the ebb. North of Adam Island there was a shift from horizonal gradients on flood to vertical gradients on the ebb. The inshore water is probably "trapped" in the bight of the harbor, i.e., with an extended residency time, while movement of water in and out the northern and southern entrances probably creates some mixing in the outer and central part of Fish Harbour. More detail of the static and dynamic characteristics of the study area and adjacent regions is provided by Smith et al. (1984).

METHODS

Most observations were made from a 5 m two-seater kayak (weather permitting), which appeared to exercise a negligible effect on the behavior of animals even at short distances (Watson 1976). A small fishing boat was used above Beaufort wind force 2, but this craft lacked the silent maneuverability of the kayak. Few publishable photographs were obtained because this species is an exceedingly difficult photographic subject. The method of making and maintaining contact was consistent throughout the study period (1 June 1970-10 September 1978). A central route from the head of Lords Cove was followed (Fig. 1); unless weather was too poor for optimal sighting in Simpson's Passage, or there was specific intent to track a group within Fish Harbour, the boat continued on track to watch-station 2 (Fig. 1). If no animals were present in Fish Harbour and conditions were less than Beaufort wind force 2, the boat would remain in the vicinity, but if the animals were already within Fish Harbour, the boat usually returned to watch-station 1 in outer Fish Harbour, from which point most of the study area normally used by porpoises could be kept under eye or binocular surveillance. As weather permitted, or presence and movements of animals dictated, this search pattern was usually repeated during the day at invervals of several hours. When porpoises were located either visually or from the sound of their expirations, the position of the boat and the initial positions of animals relative to the vessel were recorded to within a few tens of meters by taking 3-5 bearings from the many surrounding landmarks. Subsequent positions were noted in those cases when movements were tracked for extended periods, providing the animals surfaced long enough for accurate bearings to be taken and had moved to a significant distance (ca. 100 m) from the previous location. The time, location, size, and apparent composition of each porpoise group was recorded on and later transcribed from tape. The particular problems of quantifying sightings of this small cetacean have been considered by Gaskin (1977), Prescott et al. (footnote 2), Taylor and Dawson (1984), Kraus et al. (footnote 4, 1983), and Watts and Gaskin (in press). During the present study we used only data obtained in Beaufort Sea state 0-1, when visibility was unlimited within the study area and lighting was direct or diffuse, but uniform. In these ideal conditions some porpoises can be detected even from the air (250 m) at 650 m, although this is the least satisfactory method for sighting this species (Kraus et al. 1983). In a simultaneous comparison of effectiveness of stationary, mobile, and aerial observers (Kraus et al. 1983) the former, whether on land or stationary vessel, not only saw far more animals than the observers in the aircraft, but could detect them using binoculars in calm water at 1,000+ m. The probability of contact is enhanced when animals tend to surface repeatedly. The present authors found that porpoises working near the Nub close to the Simpsons Island (Fig. 1) could be clearly seen with binoculars from watch-station 1, at a distance of > 1 km in optimal conditions.

Some natural constraints on distribution of porpoises within the study area reduced the effective survey region to only 4 km^2. Virtually no animals ventured farther inshore than the shallow shelf edge (ca. 5 m) even during high water. Almost all ingress and egress was between Bean and Fish Islands (Fig. 1). Very few animals left by the southern passage from Lords Cove, and only two were ever noted to enter this way. Only one group of animals consistently visited Lords Cove in any case. No movement was noted through the narrow gut west of Hardwood Island, and only infrequent movement ($\leq$ 5%) through the passage north of Fish Island.

Harbor porpoises in the Quoddy region appeared generally indifferent to boat traffic (Watts and Gaskin in press), with no noticeable attraction bias as noted for *Phocoenoides dalli* by Kasuya and Jones (1984). Because of the small size of the study area, the impossibility of making random transects, the highly clumped distributions, and nonrandom movements of animals (see latter), any kind of line-transect approach was inappropriate. From a combination of the initial strip census search and the stationary observations, we concentrated on obtaining a "best estimate" of the mean number of animals present during each observation period with reference to each hour of the day and each tide subphase within that period. All are minimum estimates because some animals were probably missed at the seaward periphery of the study area. We tried to avoid inclusion of repeat sightings in these estimates which would lead to an upward bias, except where we calculated simple sightings of individuals per hour. The "best estimate" data were used to give relative abundance with respect to various environmental conditions, while sightings per hour were more appropriate for time-based comparisons such as relative abundance from year to year.

When sighting conditions were particularly favorable, the movements of specific groups were plotted, either by observation from one or other watch-stations which commanded a wide view with many landmarks, or by discreetly following them in the

kayak on a parallel course at distances of 50-150 m. If only one observer was present in the kayak, these periods were only included in the main data base if very few animals were known to be in the study area.

STATISTICAL ANALYSIS

For statistical analyses of these data we considered the potential application of log-linear and multivariate models, principle component analysis (PCA), factor analysis (FA), and a categorical data (χ^2) procedure. Considerable differences in the magnitude of x-variate variances would make results from PCA or FA suspect (Maxwell 1977, ch. 4). Log-linear and multivariate approaches were initially attractive, but both have disadvantages. Tests for independence of x-variates are difficult in the latter, and while these are facilitated by the former, results obtained from log-linear models are often difficult to interpret (SAS Institute Inc. 1979, p. 222). Furthermore, statistical advisers noted that use of the whole data base was contraindicated in either method because 1) there was of necessity inclusion of linear, nonlinear, and enumeration data types, and 2) there were significant numbers of empty data cells usually resulting from poor weather when operation would have been pointless. The consultants recommended use of the categorical data procedure, not only for the reasons outlined above, but also because the very nature of the x-variates (e.g., lunar cycle and tidal cycle) precluded the existence of complete independence. From the ecological point of view it was considered more important to relate one dependent variable (relative abundance of porpoises) to a group of variables one at a time than to test for independence in the latter when the result would likely be spurious.

We first determined ($P = 0.13+$) that no data set from any x-variate was significantly associated with one part of the "range" of any other by a series of simple paired χ^2 tests. The main analyses were then carried out on an IBM[5] 360 mainframe computer using the PROC FREQ program (SAS Institute Inc. 1979) which used a generalized least squares model to generate χ^2 values for combinations of the categorical levels between variables. In this case the relative abundance was related to date, time of day, tidal amplitude, tidal phase, lunar phase, extant wind direction, and wind direction 24 h previously.

To examine changes in spatial distribution within the study area, the location of 669 porpoise sightings collected in 1973-75 were plotted with respect to chronological time and time of tide. To avoid repeat sightings only the initial sighting was used in this context. To examine possible changes in distribution by depth and location, the study area was divided into three zones based on subsurface features: shallow shelving areas, subsurface slopes and scarps, and relatively deep basins and channels (Fig. 1). Such data cannot be used to deduce actual patterns of movement, but we were able to obtain some information on these through selective observations of identifiable individuals. Five of these were known to be females (consistently accompanied by calves), one a male (seen briefly copulating with a known female), and one of unknown sex. Each recorded sequential position was plotted for movements within a specific observation period, and for four of the known females data on all observations were plotted and the apparent ranges in consecutive seasons examined. In each case the master sheets had a grid with ordinates 100 m apart.

RESULTS

Hours of Observation of Porpoises in Fish Harbour Region

About 550 h of observation were made between June 1970 and September 1978, and 324 h of this were during an "intensive" study phase encompassing the summers of 1973-75. Estimates of changes in relative abundance with respect to environmental parameters were based on 181 h in optimal sighting conditions in this period (see section on Methods). Sporadic observations were maintained by our research group subsequent to 1975 or by auxilliary observers from Marine Research Associates of Lords Cove in most months except for late-December to mid-January.

Changes in Relative Abundance During the Year

From low relative abundance in the spring and late fall months, numbers of porpoises were highest during August or September in each year of the study period (Table 1). Highest values in ideal conditions were 8.00/h in Fish Harbour and 7.72/h in Simpson's Passage in September 1973 and August 1974 respectively. Observations by Marine Research Associates over the period 1971-77 in the same area, although largely of a casual nature, confirmed the animals can occur in small numbers in any month between Octo-

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sightings of harbor porpoises per hour in the Simpson's Passage and Fish Harbour areas, southern New Brunswick, 1970-78.

Month	1970	1971	1972	1973	1974	1975	1976	1977	1978
Simpson's Passage									
April	[1]0	—[2]	—	—	—	—	—	—	—
May	0.61 ± [3]0.07	0	—	0	—	—	—	—	—
June	0	0.90 ± 0.20	0.50 ± 0.15	0	—	—	—	0	0.94 ± 0.40
July	2.63 ± 0.30	1.91 ± 0.20	3.55 ± 0.40	3.55 ± 0.55	1.97 ± 0.65	1.68 ± 0.30	2.11 ± 0.30	0.76 ± 0.40	1.70 ± 0.25
August	4.42 ± 0.75	3.34 ± 0.60	6.44 ± 0.55	4.50 ± 0.60	7.72 ± 0.40	6.55 ± 0.40	3.37 ± 0.45	1.60 ± 0.25	1.93 ± 0.40
September	—	7.46 ± 1.15	6.33 ± 0.50	—	—	—	—	4.44 ± 1.00	7.47 ± 0.50
October	—	—	—	—	—	—	—	—	4.24 ± 0.02
November	—	—	—	—	—	—	—	—	0
Fish Harbour									
May	0	0	—	0	—	—	—	—	—
June	—	0	0	0.70 ± 0.01	—	—	—	0	0
July	0.93 ± 1.70	0.18 ± 0.05	3.44 ± 0.45	0.21 ± 0.04	0.46 ± 0.03	0.26 ± 0.04	0.92 ± 0.08	0.36 ± 0.15	0.22 ± 0.01
August	4.00 ± 0.78	1.04 ± 0.40	6.45 ± 0.40	4.48 ± 0.62	2.08 ± 0.70	1.94 ± 0.50	2.05 ± 0.30	1.17 ± 0.30	0.66 ± 0.08
September	—	2.41 ± 0.35	—	8.00 ± 1.80	5.22 ± 0.60	—	—	3.08 ± 1.12	0.89 ± 0.05
October	—	—	—	—	—	—	—	—	0
November	—	—	—	—	—	—	—	—	0

[1]No animals recorded. [2]No search effort. [3]Standard error of the mean.

ber and May, but probably rarely enter Fish Harbour (see next section).

Arrival and Departure of Porpoises Each Year in Relation to Sea Temperatures

First sightings in Fish Harbour were usually made in mid-late July when surface temperatures attained about 9°C, and never in Lords Cove until about mid-August despite 9°-11°C being reached at the surface in mid-late July. First regular sightings in Simpson's Passage varied from mid-May to late June. Determining the date of departure of the majority of animals from either sector was difficult because strong autumnal winds invariably interfered with observations from mid-September onwards when relative abundance was still high. In both 1977 and 1978, porpoises were still present in Fish Harbour until the last week of September and in Simpson's Passage until at least 15 October. Occasional animals may venture into the latter area in any month of the year since a very small population usually overwinters in the Quoddy region (Gaskin 1977), and one animal was sighted outside Fish Island on 7 December 1982 (B. M. Braune[6] and D. E. Gaskin, pers. obs.).

We could find no evidence that the distribution of porpoises was directly or indirectly influenced by the rather small daily local variations in sea temperatures within Fish Harbour. The most frequently observed known animal and her consorts would regularly traverse the width of the area (see Figure. 9) and their preferred locations appeared to have specific topographic rather than temperature characteristics.

Estimating Relative Abundance

Because the species does not make long dives (mean submergence 1 min 44 s, Watson and Gaskin (1983)), the required minimum period of observation needed to search the study area was not excessive. From our records we selected 3 wk in August 1972-75, when the probability of animals being present was high. In a random sample of 40 (i.e., above the minimum size for a "large" statistical sample (Bailey 1959)) search periods in optimum conditions of varying length (5 min to 2 h), the percentage of time that one or more animals was recorded increased from 50% for 10-min periods to well over 80% for 15-min periods. All observations of < 15 min were therefore discarded from the data set. If we were only interested in presence or absence, as in the case of simple locations at a given time of day or tide, observations from shorter periods or in Beaufort wind force 2+ were still of some value.

We have already outlined the methods for obtaining our "best estimates"; it is worth noting that various characteristics of the animals (e.g., short dive times, stereotyped movements, recognizable individuals) and of the study area (limited search area because of shallow water, many landmarks, shelter, and limited entry and exit points for animals) were of great assistance in reducing repeat sightings to a minimum.

[6]B. M. Braune, Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada.

Changes in Relative Abundance Between 1970 and 1978

Table 1 gives sightings of individuals per hour by month for each year from 1970 to 1978. As some observation periods were eliminated (see above) the results sometimes differ slightly from values given by Gaskin (1977) for the earlier years. Results suggest a decline in relative abundance from 1972 onwards in Fish Harbour and from 1974 onwards in Simpson's Passage. Because the 1970 values were based on a relatively short series of observations, the apparent rise from 1970 to 1971 may be spurious. The slight increase in 1978 is also suspect as most observers were less experienced than the teams used in 1970-77. The overall trend however, seems unmistakable. Furthermore, a decline in each month of the July-September period is evident when data for the whole study area are pooled (Fig. 2).

Results of the categorical data procedure tests for relative abundance of porpoises against the set of environmental parameters are presented in Table 2 (Fish Harbour) and 3 (Simpson's Passage). As might be expected, large χ^2 and significant P values were generated from the sharp drop in overall numbers sighted per observation period (regardless of its length) from 1972 to 1975, and from the great increase occurring each year between July and September. Time of day appeared to exert no influence on relative abundance in either section (P = 0.45, 0.20), nor was any statistically significant relationship noted between relative abundance and

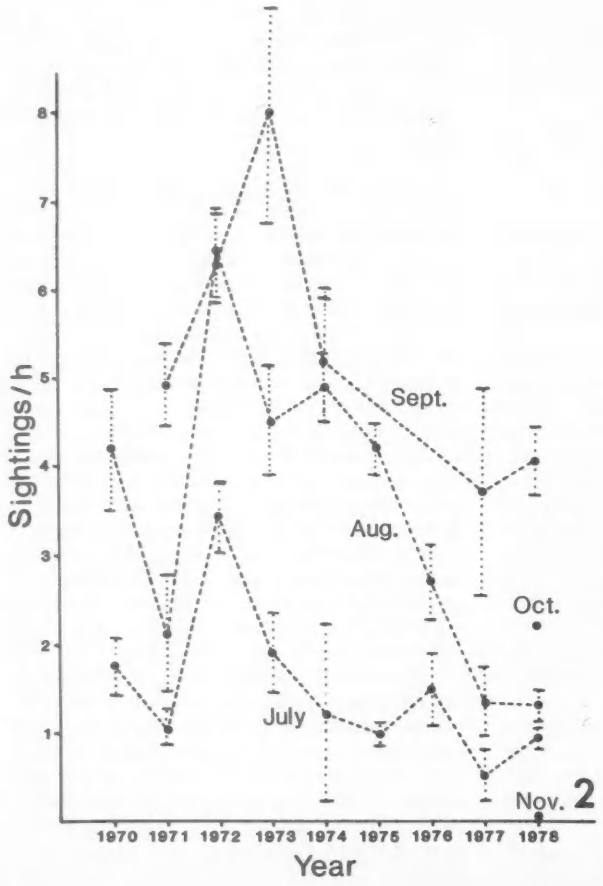

FIGURE 2.—Comparison of sightings per hour of porpoises in good condition in the Fish Harbour study area (Fish Harbour + Simpson's Passage), 1970-78 by month, from July to September. October and November values available for 1978 only. Vertical dots and bars represent standard error about the means.

TABLE 2.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. I. Fish Harbour + Lords Cove (see Figure 1). n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	249	3	39.57	0.0001*
Time of year[1] (July to early September)	249	2	63.69	0.0001*
Time of day[2] (0600- + 1900)	249	4	3.67	0.4520
Tidal amplitude[3]	249	3	7.80	0.0500*
Tidal phases[4] (Start of falling tide to end of rising tide)	249	7	3.31	0.8450
Lunar phase[5] (New moon to full moon)	249	3	5.38	0.1450
Wind extant[6] (On shore, coastwise, or offshore)	249	2	17.58	0.003
Wind 24 h previous[6]	249	2	12.22	0.0094

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.
[2]Four periods of 3 h each, post-1900 observations amalgamated.
[3]Four subphases (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).
[4]The eight subphases given in Figure 4 were used.
[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.
[6]Four subdivisions used. More subdivision than these resulted in many empty data cells.
*Statistically significant at 0.05 level or better.

TABLE 3.—Results of categorical data procedure tests for observed numbers of harbor porpoises in comparison to expected numbers with different environmental parameters in the Fish Harbour region of southern New Brunswick, 1972-75. II. Simpson's Passage. n = observation periods; χ^2 = two-way table statistic.

Parameter measured	n	df	χ^2	P
Years (1972-75)	132	3	7.58	0.050*
Time of year[1] (July to early September)	132	2	16.99	0.0002*
Time of day[2] (1600- + 1900)	132	4	5.98	0.201
Tidal amplitude[3]	132	3	2.54	0.468
Tidal phases[4] (Start of falling tide to end of rising tide)	132	7	9.97	0.190
Lunar phase[5] (New moon to full moon)	132	3	7.38	0.061**
Wind extant[6] (Onshore, coastwise or offshore)	132	2	0.95	0.620
Wind 24 h previous[6]	132	2	0.93	0.628

[1]Categorical division of three periods (July, first 3 wk of August, last 1½ wk of August + early September) to balance effort.
[2]Four periods of 3 h each, post-1900 observations amalgamated.
[3]Four subphase (≥ 5.5, 5.6-6.5, 6.6-7.5, ≥ 7.6 m).
[4]The eight subphases given in Figure 4 were used.
[5]Three subdivisions used. More subdivision than these resulted in many empty data cells.
[6]Four subdivision used. More subdivision that these resulted in many empty data cells.
*Statistically significant.
**Close to significance at 0.05 level.

magnitude of tidal amplitude in Simpson's Passage. In shallower, semi-enclosed Fish Harbour however, significantly more porpoises were present (P = 0.05) at low tidal amplitudes (≤ 6.5 m) than high amplitudes (≥ 6.6 m). Data for the most commonly sighted individual (a female with a large dorsal scar) corroborated this general finding; about 78% of all sightings of this animals were made when the amplitude was 6.5 m or less.

Relative abundance did not alter (P = 0.84, 0.19) in either zone of the study area during the tidal cycle. Similarly no significant change occurred relative to the lunar phase in Fish Harbour, although in Simpson's Passage the χ^2 value approached the arbitrary 0.05 level of significance (P = 0.061; n = 249). No relationship between extant or previous wind direction was evident in Simpson's Passage (P = 0.62, 0.63; n = 132), but there appeared to be a significant association between wind direction and relative abundance of porpoises in Fish Harbour (P = 0.0003, 0.009; n = 249). In both cases far more animals were present during onshore wind directions than when winds were coastwise or offshore.

Distribution and movements of porpoises on the fine scale is likely to be correlated with the presence or absence of food species which, in the Quoddy region, consist largely of juvenile herring, *Clupea harengus*; mackerel; and small gadoids (Smith and Gaskin 1974). The dispersal of the former in this region is greatly influenced by current velocities (Jovellanos and Gaskin 1983). Unfortunately the beam width of available equipment was far too narrow to permit us to cover the study area by acoustic survey thoroughly, or even representatively, at any given time or tide phase. Because one of our major aims at the outset of the study was to avoid disturbing normal behavior of the porpoises, it was also rarely possible to acoustically scan in their immediate vicinity. We were however able to infer feeding behavior from diving patterns (e.g., "pattern B") carried out consistently in one location (Watson and Gaskin 1983). Sometimes fish were seen jumping at the surface in such areas (Fig. 3), and these zones were acoustically scanned on an opportunistic basis. Fish schools, recorded during bottom topographic acoustic mapping runs, tended to be concentrated at several locations in which porpoises were often sighted. Usually these traces were of herring school-type. While this species predominates in the Quoddy region in the summer months (Jovellanos and Gaskin

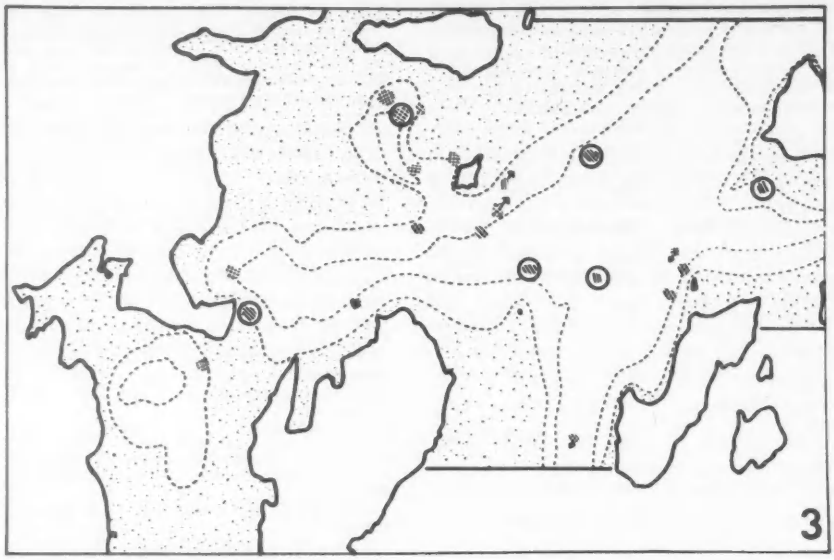

FIGURE 3.—Locations in Fish Harbour at which fish were detected visually or by sonar in 1973-78; opportunistic records only. Stipple: species not identified; vertical bars: Atlantic mackerel; diagonal bars: Atlantic herring; circles: one or more porpoises simultaneously present with record; arrows: direction of fish movement. The size of hatched areas indicates approximate size of the school.

1983), some could have been of harbor pollack, which are also taken by this species.

Changes in Distribution Within the Fish Harbour Region

No differences in distribution of the 669 recorded sighting positions for 1973-75 could be detected when they were plotted either by four or eight time periods from 0600-2200, but considerable differences were evident when they were plotted against eight subphases (slack low, slow flood #1, fast flood, slow flood #2, slack high, slow ebb #1, fast ebb, and slow ebb #2) of the tidal cycle. This analysis ignores for the moment the fact that many animals move in a rather regular manner through the study area, since useful information can be obtained simply from noting where they are at any given time of tide. The results (Fig. 4) showed that up to 80% of porpoises were congregated over the shallow shelf margins, slopes, and scarp areas between the onset of flood tide and high water. Conversely, about the same proportion became concentrated over the basin and channel areas between onset of the ebb, and slack low water.

The Nature of Movements Within the Fish Harbour Region

It became evident that when the recognizable animals returned each year they reestablished "specific ranges" (for lack of a better term) in virtually the same locations in Fish Harbour each summer (Figs. 5-8). There is some evidence that these "ranges" shifted progressively further east of Deer Island between 1973 and 1975, especially in the case of the scarred female mentioned earlier. Each of these areas in Fish Harbour, of which we were able to measure nine approximately, appeared to be about 1.0-1.5 km^2 in extent. Even the most distinctive animals would disappear from the study area for extended periods and then reappear again, just as Gaskin et al. (1975) noted for a female carrying a radiotelemetric package. The scarred female was once observed with a calf off the eastern coast of Simpson's Island, and on another occasion between Minke Ledges and Tinker Island, which lie between 1 and 3 km south of the main study area. This specimen was present in the Fish Harbour region for about half the days of excellent visibility in 1973-75, was well known to all observers, and yet was only

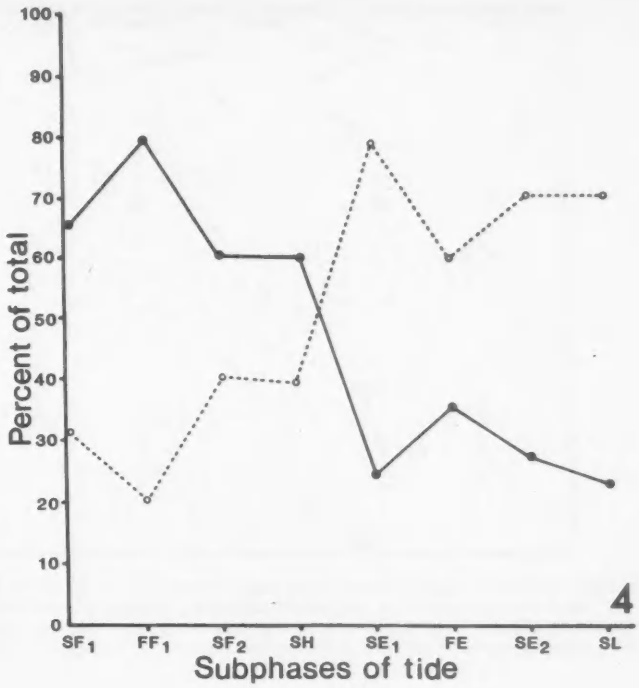

FIGURE 4.–Distributions of 669 harbor porpoises in Fish Harbour 1973-75 over subsurface topographic features, by eight subphases of the tide: Slack low water (SL), slow flood 1 (SF_1), fast flood (FF), slow flood 2 (SF_2), slack high water (SH), slow ebb 1 (SE_1), fast ebb (FE), and slow ebb 2 (SE_2). Solid line shows percentage over shallow shelf, scarps, and slopes; dotted line, percentage over basins and channels.

seen on the two above occasions during simultaneous surveys outside the present study area.

Only in the case of this particularly distinctive animal were we able to obtain enough observations to map some of her patterns of movement over extended periods. On 17 August 1973, for example, we tracked her for 2 h 12 min (57 position fixes, Fig. 9), noting that she tended to stay close to the slopes of the main basin-channel, with one foray around the small basin in Lords Cove. This kind of point-to-point travelling interspersed with short periods of submergences in one location is quite typical of this species. This animal repeated almost identical range movements on 13 and 29 August 1974. On 1 and 30 August 1974 (1 h 4 min and 3 h 3 min respectively) this animal spent far longer periods in relatively restricted locations (Fig. 10). Submergences were again of the "pattern B" type, and no surface resting was recorded. On 1 August many herring were seen jumping at the surface immediately after each submergence by the female. Her calf was often left at the surface during these bouts.

"Systematic patrolling" of small areas, often in the lee of ledges or small islets was also recorded (Fig. 10). The movements illustrated were carried out by a school of three medium-sized animals accompanied by one small one on 2 August 1974. The group sychronously dove repeatedly while moving back and forth in one restricted scarp location, then abruptly travelled to the second location shown and repeated the pattern.

DISCUSSION

The distribution of some small odontocetes is known to be correlated with sea surface temperatures (Gaskin 1968; Würsig and Würsig 1980), but the relationship is almost certainly indirect, the result of influences exerted one or more levels further down the food chain. The entry of the main summer population of harbor porpoises into the study area not only coincides with 9°-10°C surface temperatures, but also with the arrival of large numbers of juvenile herring which feed in the Quoddy region during the summer months (Battle et al. 1936; Jovellanos and Gaskin 1983). Although transport of relatively small fish into the study area might be expected to be at a maximum during spring tides,

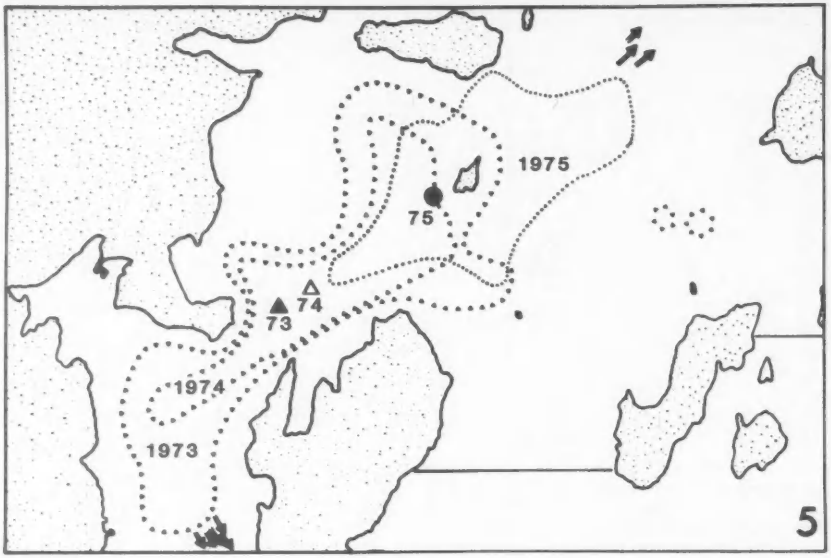

FIGURE 5. – Broken lines encompass all sightings of recognizable animal (#1, scarred mother). 1973: solid wedges; 1974: open wedges; 1975: dots. The solid triangle, open triangle, and solid circle respectively represent the center of the "range" as determined by the mean of the latitudes and longitudes of each position, excluding single isolated sightings. Arrows indicate number of times this animal (and any consorts) were observed leaving the "range". In each case they were swimming at 4+ knots and outdistancing the kayak.

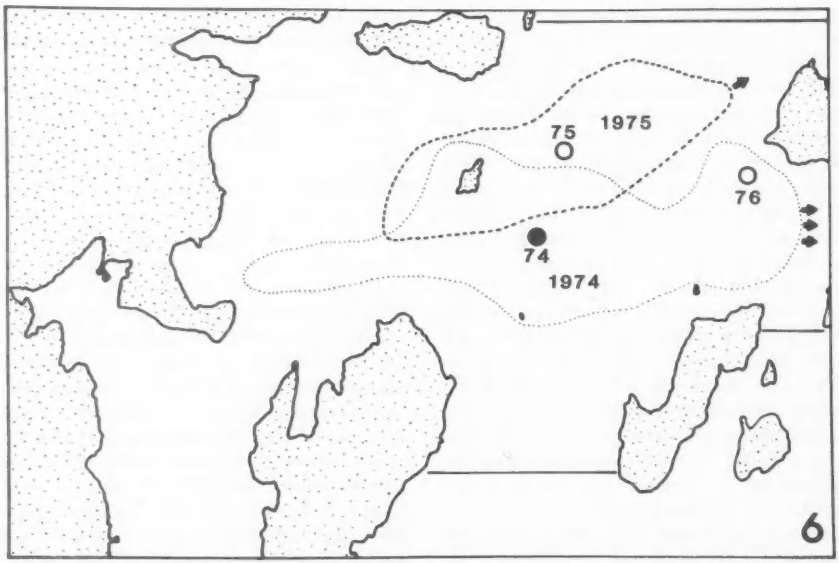

FIGURE 6. – Broken lines encompass all sightings of known animal #2 (clipped fin). 1974: dotted lines; 1974: dashes. Open circle and closed circle for 1974 and 1975 respectively, and arrows indicating animal leaving the area are as in Figure 5.

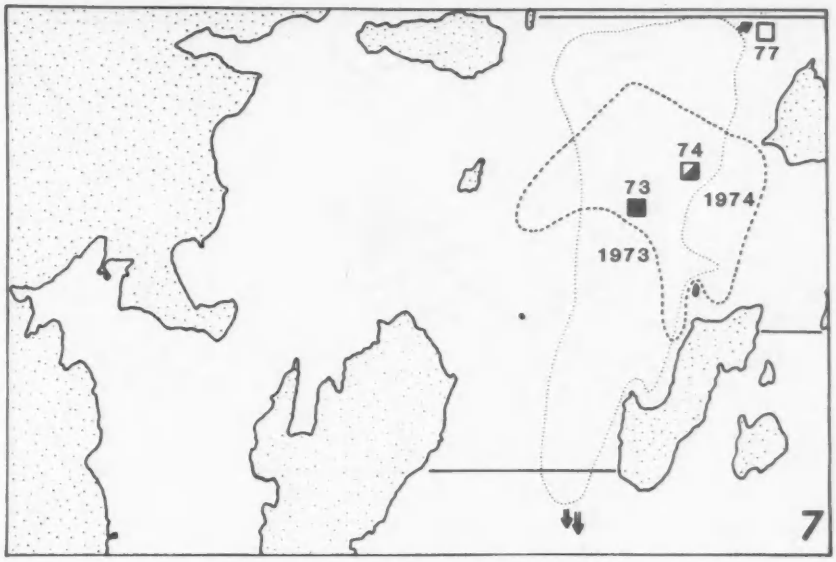

FIGURE 7. – Broken lines encompass all sightings of known animal #3 (Simpson's Passage mother) except for single 1977 sighting. 1973: dotted line; 1974: dashed line. Other symbols as in Figure 5.

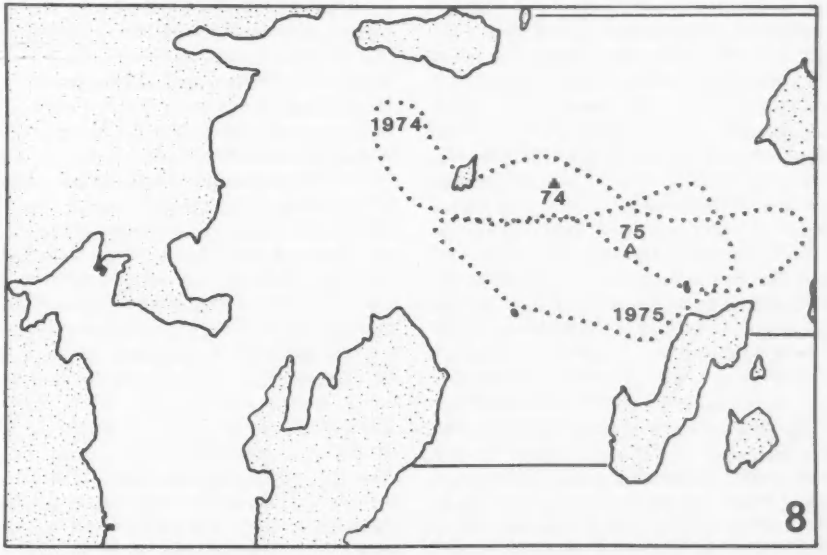

FIGURE 8. – Broken lines encompass all sightings of known animal #4 (Light brown mother). 1974: solid wedges; 1974: open wedges. Other symbols as in Figure 5.

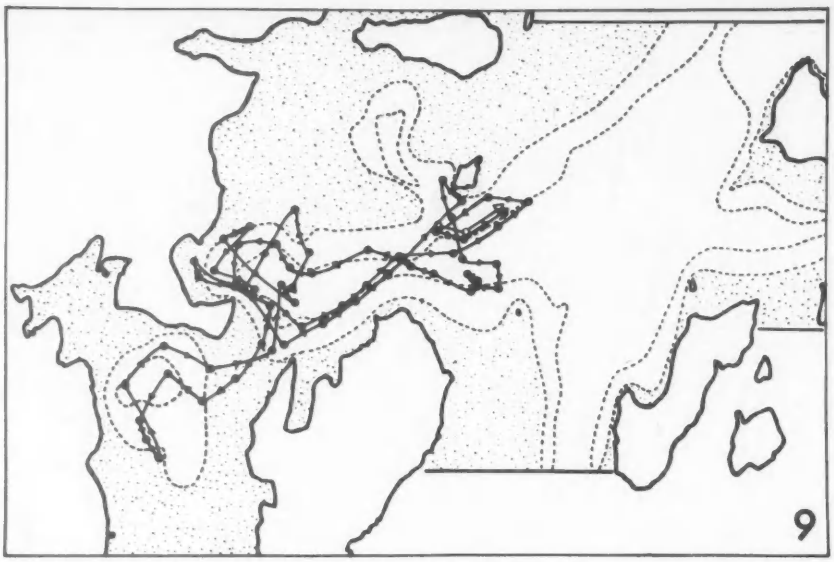

FIGURE 9.—Movements of scarred mother during 2 h 12 min period of 10 August 1973 accompanied by calf (57 position fixes). On some occasions they resurfaced close to an immediately previous position; about 75 surfacings are represented by these positions. Reverse arrow indicates initial contact point (just outside Lords Cove), solid arrow point where tracking was abandoned, and white circles position of a medium-sized animal which briefly joined the pair.

we found relative abundance of porpoises conversely to be greatest during neap tides. About 63% of the sightings in 1973-75 were of mothers and calves. Possibly these animals stay out of semi-enclosed areas during periods of maximum water transport, especially in areas with turbulent shallows such as the Fish Harbour region. On the other hand, if there are larger numbers of herring schools moving into the outer part of the Quoddy region it may not be necessary to forage in inshore waters. Once the animals are in the study area however, the observed changes in distribution during the tidal cycle confirm the earlier subjective comment (Watson 1976) that porpoises seemed to move inshore with the flood tide and offshore with the ebb.

The distribution of porpoise activity in the region appeared to be closely related to subsurface topography, particularly the margins of the basins and channels in areas of restricted water flow, the lee of islets, especially Fish Island and the Nub, and blind trench heads such as that just north of Hathaway Head. Because our meager acoustic records revealed fish traces in all these sites at one time or another (Fig. 3), we speculate that these may be areas of fish accumulation which the porpoises have learned to exploit. Each may have subsurface eddies or areas of relatively slack water against the lee side of the slope or near the bottom, in which fish can shelter from strong currents, and in which zooplankton might also accumulate. In such areas fish could not only avoid being carried further inshore, but could also feed (Hamner and Hauri 1977). Dispersal from offshore areas into the coastal belt is likely to be augmented by onshore winds, which can increase significantly the flow of water in the immediate surface layers. Local fishermen believe that offshore winds serve to hold "feed" away from the coast, while coastwise winds might reduce the possibility of entry into Fish Harbour by increasing surface flow past the relatively narrow passages. We conclude that light or moderate winds are unlikely to affect any small cetacean directly; when winds were strong enough that behavior might conceivably be affected, we were not usually operating.

Large variation always occurs in data such as these, and it is to a large extent unpredictable. Such variation in relative abundance can be explained quite simply; these animals are large, highly mobile predators with sophisticated adaptations both for active and passive acoustic scanning for their equally

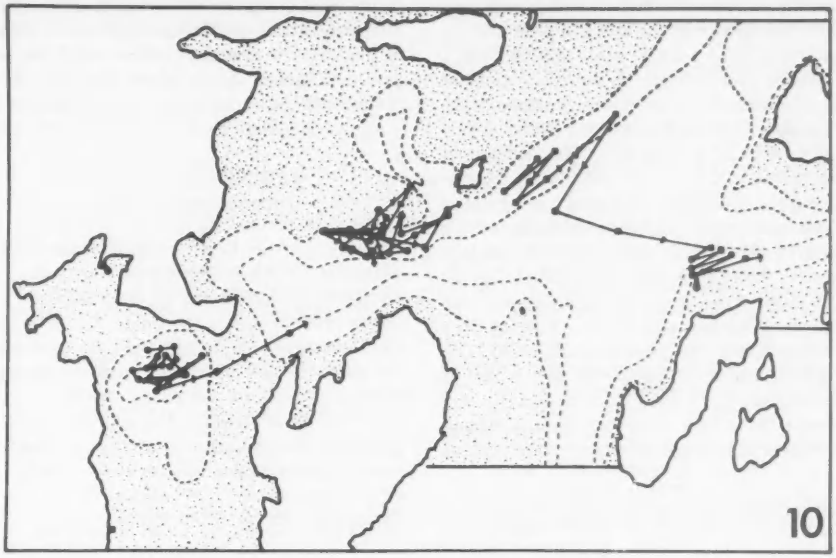

FIGURE 10. – Movements of scarred female on 30 August 1974 (solid circles at left of figure) and 29 August 1974 (solid circles in center of figure). Solid squares show "patrolling" behavior of school of four animals recorded on 2 August 1974. Qualifying comments on position fixes and surfacings in Figure 9 apply here also.

mobile prey. That the harbor porpoises in this area can shift tens of kilometers in a few hours cannot be questioned (Read and Gaskin in press); if few fish are present in one area, they may well move in a loosely synchronized group to forage in other localities. This degree of mobility and scanning ability is highly adapted not only to the mobility of their prey species, but also to the patchy nature of the distribution patterns of such fish; there is probably a significant random element in the dispersal of juvenile herring in the Quoddy region (Jovellanos and Gaskin 1983). The type of porpoise movement shown in Figure 9 was presumed to indicate that prey were dispersed, since the animal spent little time in any one location. In the other movement pattern (Fig. 10) the same animal was believed to be encountering prey in local concentrations that merited prolonged submergences in one area.

We have little evidence that the region might be significant either as a mating area or a calving ground. Females appear to have their calves offshore, since, although the latter may be very small in late June and July, they already accompany females sighted in the outer part of the Quoddy region (Smith and Gaskin 1983). Many females with calves appear to remain on tidal convergence streaks up to 20 km offshore in the outer Quoddy region (Read 1983) and may not move into the coastal zone at all. It seems more likely that the study area functioned as a significant feeding area for this species rather than being a zone favoured for reproductive activity.

The demonstrated existence of "specific ranges" and annual returns by individual harbor porpoises in this study is not surprising. Rather similar patterns, although sometimes on very different geographical scales, have been recorded for *Delphinus delphis* by Martin et al. (1971), *Orcinus orca* by Bigg (1982), *Tursiops truncatus* by Wells et al. (1980) and Würsig and Würsig (1979), and *Lagenorhynchus obscurus* by Würsig and Würsig (1980). Periodic disappearances and abrupt reappearances of *T. truncatus* were also recorded by Würsig (1978), while studying the animal.

With respect to the progressive decline in relative abundance in the peak part of summer, lack of consistent observations through late September-late October (because of high winds) prevented us from determining whether or not this resulted from a real population decrease in the area, or simply a shift of peak abundance from mid-August to mid-September during the decade. Consequently we adopted an indirect approach to the problem, plotting sightings

per hour for each month of summer for each year with sufficient data (Fig. 2). This suggests that the decline resulted from a combination of both factors, with a general overall decline in relative abundance since about 1973 and a progressive retardation of the peak of numbers since about 1975. Unfortunately there is insufficient information in Department of Fisheries and Oceans records to decide if any change in food supply could have occurred during those years, especially with respect to juvenile herring abundance (T. D. Iles[7]). Nevertheless, our surface temperature records for the inner Quoddy region reveal a consistent decline in the mean summer value (centered on mid-August) from above 12°C in 1971 to below 11°C in 1977 (Gaskin et al. 1979). The temperature curve is compared with the pattern of relative abundance in Figure 11; there is close correspondence from 1972 onwards. Such a decline might result from increase in relative dominance of Nova Scotia current water in the Bay of Fundy (Sutcliffe et al. 1976) and perhaps a significant decline in the availability of zooplankton prey of juvenile herring. Alternatively the slightly cooler waters might be marginally less suitable for young porpoise calves.

[7]T. D. Iles, Biological Station, Department of Fisheries and Oceans, New Brunswick, E0G 2X0, Canada, August 1980.

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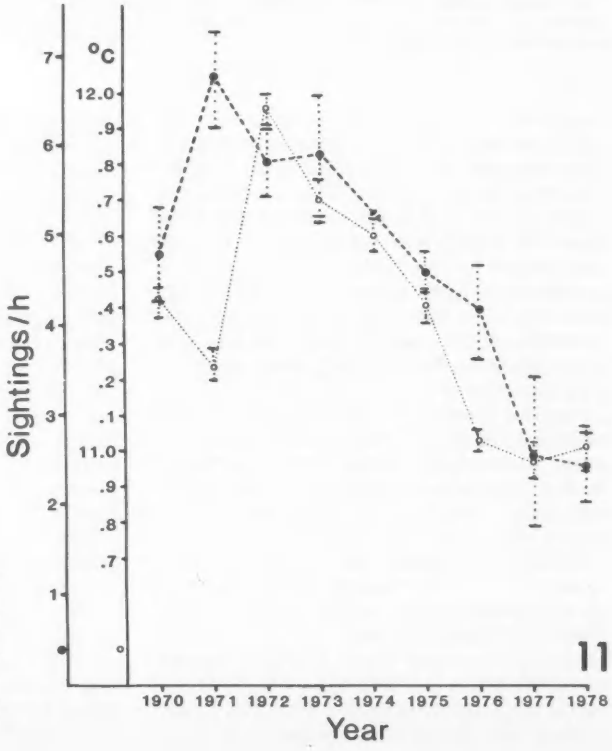

FIGURE 11.—Comparison of midsummer (late July-early September) sightings per hour of harbor porpoises in the Fish Harbor region of New Brunswick between 1970 and 1978 with surface temperatures based on 8 stations (n = about 60/annum): Solid circles and dashed line (sightings per hour), open circles and dotted line (°C). Vertical dots and bars represent the standard error about the mean.

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NOTES

THE RELATIONSHIP BETWEEN TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, ABUNDANCE AND SEDIMENT COMPOSITION OFF GEORGIA

Elucidation of the relationship between physicochemical factors and fish abundance has long been of interest to fisheries biologists. For example, water temperature frequently exerts a strong influence on the abundance of many pelagic marine fishes (Radovich 1961; Laurs et al. 1977; Barkley et al. 1978; Moyle and Cech 1982), and this effect has been noted also for freshwater species (Magnuson et al. 1979; Moyle and Cech 1982). For benthic marine fishes, however, substrate composition may be a more important factor affecting fish abundance and distribution. Associations between abundance and substrate composition have been noted for a diverse group of fishes: agonids, bothids, cottids, pleuronectids, scorpaenids, and steichaeids (Day and Pearcy 1968; Powell and Schwartz 1977; Marliave 1977; Barton 1982). Where detectable, however, these associations vary substantially in intensity. This is probably due to the fact that many physicochemical factors are intercorrelated and most fishes probably respond to intercorrelated suites of variables rather than to single factors alone.

In this note we quantify the relationship between catch rate of a demersal species, the tilefish, *Lopholatilus chamaeleonticeps*, and substrate composition. This species is commercially exploited throughout most of its range (Grimes et al. 1980; Low et al. 1983; Turner et al. 1983), although, prior to this study, tilefish resident to the continental slope off Georgia appeared to have been subjected to minimal exploitation (D. Harrington[1]). The elucidation of a substrate-abundance relationship for tilefish should aid in the management and harvest of this species.

Methods

A total of 19 bottom longline sets and 19 sediment samples were obtained during daylight hours, between 5 May and 22 November 1982. Fourteen longline sets, each comprising 1.6 km of line, and 12 sediment samples (Table 1) were obtained from the RV *Georgia Bulldog* (University of Georgia Sea Grant Program vessel). Five sets ($\bar{X} \pm 1$ SD length = 0.31 $\pm$ 0.09 km) and seven sediment samples were collected aboard the RV *Delaware II* (National Marine Fisheries Service vessel). At least one of the authors was present during collections.

Bottom longlining on the *Georgia Bulldog* was conducted using snap-on gangions ($\sim$ 0.5 m in length) spaced about 4 m apart, along a 6.3 mm diameter galvanized aircraft cable groundline. Gangions were equipped with 4/0 or 5/0 circle hooks and baited with either fish or squid. A similar system was employed on the *Delaware II* except that a much shorter groundline of 6.3 mm diameter hardlaid nylon was used (Table 1), with hook sizes ranging from 3/0 to 8/0.

Substrate Analysis

Substrate samples were collected with a 25 $\times$ 30 $\times$ 37.5 cm box dredge suspended from a power winch. The dredge was lowered to the bottom and then dragged across the substrate (typically for $<$ 5 min). After retrieval, 1.2-2.0 kg of sediment were removed from the dredge and stored in plastic bags. It is assumed that these samples accurately reflect the composition of surface sediments.

Sediment samples varied in their proximity to longline sets. Fourteen samples were taken at the end of longline sets. Of the remaining five samples, one was taken from the midpoint of a set, three were taken alongside sets within a distance of 0.2 km, and one was taken alongside a set at a distance of 0.6 km. The general area sampled (see Table 1 for loran C coordinates) has a relatively homogenous, low-relief bottom topography, and large variations in substrate composition probably do not occur over short distances (V. J. Henry[2]).

To determine the fraction of each sample composed of sand and silt-clay, a known amount of sediment (i.e., enough to yield a dry weight of between 60 and 100 g) was dried in a forced-air oven at 98°C until a constant weight was reached. The sample was then moistened with water which contained $\sim$ 2 g of Calgon[3] as a dispersant, and washed through a sieve which retained particles $\geq$ 0.0625 mm (4ϕ) (U.S. standard seive #230). Sediments retained by the sieve were then oven-dried to a constant weight to

[1]D. Harrington, University of Georgia Marine Extension Service, Brunswick, GA 31523, pers. commun. 1983.

[2]V. J. Henry, Dept. of Geology, Georgia State University, Atlanta, GA 30303, pers. commun. 1983.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sediment composition and catch data for longline sets used to establish the relationship between catch rates and sediment composition off Georgia.

Date	Loran C coordinates	Minimum and maximum depths (m) of longline sets	Groundline length (km)	Number of hooks	Soak time (h)	Tilefish per 100 hook-h^{-1}	Percent sand (≥4ϕ)	Percent silt-clay (<4ϕ)
5-5-82	45086.1 60777.3	187-190	1.61	242	3.3	2.11	[1]58	42
5-29-82	45092.9 60743.2	193-194	1.61	390	4.3	1.72	53	47
5-29-82	45093.8 60729.9	[2]196	1.61	348	5.3	3.29	[1]49	51
5-30-82	45088.0 60869.4	140-143	1.61	284	3.5	0	85	15
5-30-82	45080.8 60864.2	164	1.61	330	4.2	0	69	31
5-30-82	45076.8 60854.7	182-185	1.61	247	4.0	0.41	64	36
5-30-82	45073.0 60847.0	203	1.61	254	3.6	0	64	36
5-30-82	45069.6 60841.0	219	1.61	298	2.9	0.57	79	21
6-29-82[3]	44736.5 61531.7	No data	0.18	50	2.5	0	88	12
7-1-82[3]	45039.6 60974.6	199	0.35	100	2.0	0	69	31
7-2-82[3]	45065.4 60868.6	No data	0.35	100	1.0	0	80	20
7-12-82[3]	26979.6 39551.5 (9960-chain)	216-223	0.35	103	1.0	0	98	2
7-24-82	45109.8 60548.5	186-187	1.61	258	3.2	3.56	[1]40	60
7-25-82	45101.0 60549.0	217-219	1.61	241	4.0	3.80	48	52
8-13-82	45076.0 60842.6	195-201	1.61	266	3.0	0.50	74	26
8-14-82	45085.6 60735.0	230	1.61	352	3.7	2.98	57	43
8-17-82	45093.8 60555.9	255-258	1.61	245	3.9	1.67	55	45
11-22-82	45097.8 60720.5	186	1.61	311	3.5	3.95	[1]48	52
11-22-82	45095.8 60716.0	189-191	1.61	250	2.9	5.34	52	48

[1]Substrate samples were taken during a different cruise, however, samples were always taken within 65 d of each other.
[2]A single depth measurement means that only one reading was taken during the longline set. This depth is an approximation of longline depth.
[3]Samples taken from the *Delaware II*.

determine the percentage of sand and larger particles in the sample. The silt-clay fraction was obtained by subtraction. Replicate subsamples were taken from six collections to establish the technique's precision. The mean difference in percent silt-clay fraction among the six replicates was 2.5% (s = 1.4%). A t-test for paired samples indicated that significant differences did not exist among replicate determinations for a given sample (t = 0.30, df = 5, $P > 0.7$).

Statistical Analysis

To determine the relationship between tilefish catch rate and sediment composition, we used the silt-clay fraction of each substrate sample as an independent variable (X) and catch rate (i.e., tilefish caught/100 hook-h per soak time) as the dependent variable (Y). Exponential and polynomial regression models were fit to the data using the SAS statistical programs (SAS Institute Inc. 1982). The best polynomial model was compared with the nonlinear exponential model using R^2 as the criterion for model performance. Similar patterns of variation were observed in plots of residuals from all models, hence R^2 values are a reasonable criterion for model selection.

Results

The size structure of tilefish caught off Georgia was typical of unexploited to lightly exploited tilefish stocks (Grimes et al. 1980; Turner et al. 1983). This size structure remained relatively constant for ~ 10 mo, after which a slight decrease in catch rates and a possible truncation of size structure were observed (authors' unpubl. data). These results confirm verbal reports that little exploitation has occurred off Georgia (Harrington footnote 1). Hence, the data used in this analysis were probably not influenced by prior exploitation.

A total of 323 tilefish were taken on 19 longline sets (Table 1). Catch rates ranged from 0 to 5.34 tilefish/100 hook-h. Parameter estimates for linear and quadratic terms of the polynomial regressions were significantly different from zero (Table 2). Inclusion of a cubic term, however, did not significantly improve ($F = 0.75, P > 0.40$) the fit which was obtained using a second-degree polynomial. The second-degree polynomial yielded a higher R^2 value than the nonlinear exponential model (Table 2) and hence was deemed to be the model of best fit. The y-intercept of this model also was not significantly different than zero (Table 2, Fig. 1) which contributes to its biological realism. Using this equation, 74% of the variation in catch rate could be accounted for by substrate composition alone.

TABLE 2.—Comparison of regression models. Either F-tests (b_1), t-tests (b_0), or asymptotic confidence intervals (exponential model) were used to test the significance of parameters.

Model	b_1	b_0	R^2
$y = 0.087X - 1.496$	**	*	0.64
$y = 0.155(e^{0.058X})$	*	ns	0.68
$y = 0.002X^2 - 0.050X + 0.122$	***	ns	0.74

ns = nonsignificant
* = $P < 0.05$
** = $P < 0.001$
*** = $P < 0.0001$

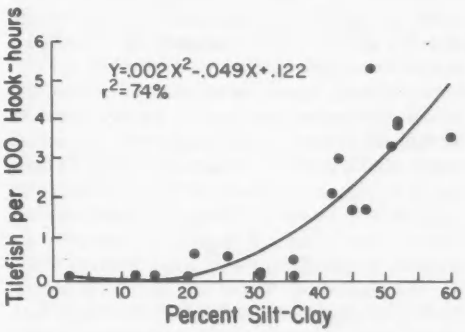

FIGURE 1.—Relationship between the silt-clay fraction of the sediments and tilefish catch rates off Georgia, U.S.A.

Discussion

Tilefish abundance, as estimated by catch rates off Georgia's continental slope, was strongly correlated with the silt-clay fraction of the substrate. This relationship was nonlinear, and based on R^2 values, a second-degree polynomial regression provided the best fit to the data. Off the northeastern United States, tilefish also were most abundant on fine-grain sediments (Able et al. 1982), although they were also found in horizontal burrows in the sides of submarine canyons (Warme et al. 1977), and in boulder fields (Valentine et al. 1980). Because tilefish construct vertical burrows in the substrate (Able et al. 1982), they require sediments which possess sufficient stability to prevent the collapse of their burrows. It would appear that bottom areas off Georgia which contain a sand fraction > 60% do not support substantial tilefish densities (Table 1, Fig. 1). It is likely that such substrates are not stable enough to allow tilefish to construct burrows. Thus, the observed correlation between catch rate and substrate composition has a biologically realistic explanation: substrates with high silt-clay fractions are conducive to the construction and maintenance of tilefish burrows, while substrates with high sand fractions are not. A similar explanation, based on submarine observations, has been proposed by Able et al. (1982) to explain tilefish distributions off the northeastern United States. Although we have not observed tilefish burrows off Georgia, they have been identified in soft bottom areas off South Carolina (R. Jones[4]).

While the relationship between catch rates and sediment composition is quite strong, several potential sources of error exist in our data. First, catch rate data were collected from two different vessels using different gear. Pooling data from the different vessels, however, would tend to obscure the relationship between catch rates and sediment composition. Hence, if differences in sampling methods did have an effect on our data, it would make the estimates of the catch rate-sediment relationship conservative.

Second, only one substrate sample was collected with each longline set. While quantification of

[4]R. Jones, Harbor Branch Foundation, Fort Pierce, FL 33450, pers. commun. 1983.

geographical variation in substrate composition was beyond the scope of this project, low relief areas off Georgia generally do not display large variations in substrate composition (Henry footnote 2). Evidence to substantiate this point is presented in Table 1, as substrate samples from areas with similar loran coordinates typically possessed similar substrate compositions.

Third, while a seasonal component to catch rate has been observed off New Jersey (Grimes et al. 1980), our data for this analysis do not strongly display this trend (Table 1).

In addition, because the area fished did not display evidence of significant prior exploitation, our results were not affected by the potentially confounding influence of commercial fishing.

In conclusion, approximately three-quarters of the variation in tilefish catch rate off Georgia could be attributed to variation in a single physicochemical factor: the silt-clay fraction of the substrate. At present, however, the generality of this relationship is unknown with respect to other geographical areas or locations with different exploitation histories. In addition, temperature also has been shown to affect the distribution of tilefish off the northeastern United States (Grimes et al. 1980). It is likely that within areas possessing suitable thermal regimes, substrate composition is a major factor affecting tilefish abundance. While a variety of associations between fish abundance and physicochemical factors have previously been identified (Moyle and Cech 1982), to our knowledge, none approach the intensity of the relationship described herein. We believe that identification of this relationship will aid fisheries biologists in the identification and demographic quantification of tilefish stocks as well as the location of new fishing grounds.

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GARY D. GROSSMAN
MICHAEL J. HARRIS
JOSEPH E. HIGHTOWER

School of Forest Resources
University of Georgia
Athens, GA 30602

THE DEVELOPMENT AND OCCURRENCE OF LARVAE OF THE LONGFIN IRISH LORD, *HEMILEPIDOTUS ZAPUS* (COTTIDAE).

The subfamily Hemilepidotinae, endemic to the North Pacific Ocean, is one of the more generalized subfamilies within the Cottidae (Peden 1978). According to Peden (1978), the subfamily is composed of three subgenera: 1) *Calycilepidotus* which includes *Hemilepidotus spinosus*; 2) *Hemilepidotus* which includes *H. hemilepidotus*, *H. jordani*, *H. zapus*, and *H. gilberti*; and 3) *Melletes* which includes *H. papilio*. The early life histories of most species are inadequately known and separation of larvae in mixed samples is difficult. Gorbunova (1964) described a number of larval series which she labeled *H. hemilepidotus*, *H. gilberti*, *H. gilberti zapus*, *H. jordani*, and *H. papilio*,[1] but these descriptions are incomplete as well as incorrect for several species (Peden 1978; Richardson and Washington 1980). Hattori (1964) described a series of *H. gilberti* larvae (7.1-32.5 mm), and Peden (1978) illustrated postlarvae (> 18 mm) of *H. hemilepidotus*, *H. spinosus*, *H. zapus*, and *H. jordani*. Richardson and Washington (1980) described larvae of *H. hemilepidotus* and *H. spinosus*. We here provide the first complete description of *H. zapus* larvae, and include comments on larval occurrence in the eastern Bering Sea. This work supplements and clarifies the work of previous researchers by providing diagnostic characters useful in distinguishing the species.

MATERIALS AND METHODS

Specimens of *H. zapus* used in this study were collected during ichthyoplankton surveys conducted in the Bering Sea by the Northwest and Alaska Fisheries Center between 1977 and 1980. Morphological measurements were made on 57 unstained larvae (6.7-22.0 mm SL) following Matarese et al. (1981), except depth at caudal peduncle which was measured at the point of least depth. Measurements were grouped by 1 mm SL intervals, and the means of the measurements within each interval were plotted as percentage of the mean of standard lengths or head lengths within the interval (Kendall and Vinter 1984). A computer-generated best nonparametric curve, based on all data points, was drawn to illustrate relative growth trends. Counts of meristic structures were made on 13 specimens differentially stained according to Dingerkus and Uhler (1977) following procedures outlined in Matarese et al. (1981). Terminology of head spination generally follows Richardson and Laroche (1979) and Richardson and Washington (1980). Illustrations were made by the junior author with a camera lucida, and all specimens were preserved in either 3% Formalin[2] buffered with sodium borate or 100% glycerin.

Identification of *Hemilepidotus zapus*

We have routinely collected three types of Hemilepidotinae larvae during ichthyoplankton surveys in the eastern Bering Sea (1977-80). According to Peden (1978), four species of adults occur in this area: *Hemilepidotus hemilepidotus*, *H. jordani*, *H. zapus*, and *H. papilio*. Although preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated, we can separate the two species at notochord flexion according to differences in external pigment along the posterior body. *Hemilepidotus hemilepidotus* larvae develop pigment above the notochord along the posterior body earlier and in greater density than larvae of *H. jordani* (Fig. 1A, B). Initially, the third series of larvae (< 17.0 mm SL) was misidentified as *H. papilio* (see Waldron and Vinter[3]) based on the presence of urostyle pigment (Gorbunova 1964). With the acquisition of larger specimens, > 17.0 mm SL, the complete series was later identified as *H. zapus* based on a set of characters taken in part from Peden (1978) (Table 1). Gorbunova's (1964) specimen attributed to *H. zapus* lacks pigment on the urostyle; of her two illustrations of *H. papilio* (footnote 1) only the 10.7 mm SL

[1] *Hemilepidotus papilio* (= *Melletes papilio* from Gorbunova (1964)).

[2] References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

[3] Waldron, K. D., and B. M. Vinter. 1978. Ichthyoplankton of the eastern Bering Sea. Unpubl. manuscr., 77 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard E., Seattle, WA 98112.

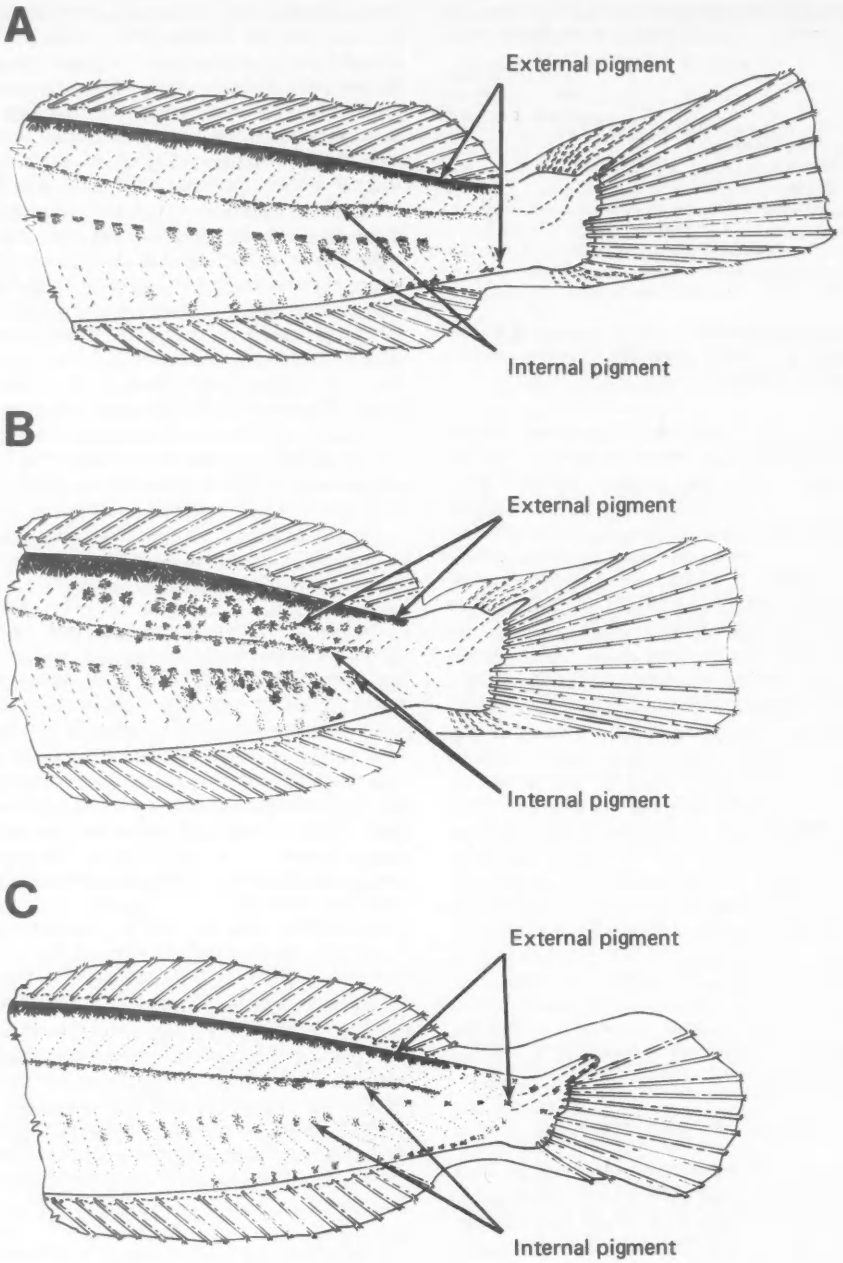

FIGURE 1. – Postanal pigment patterns in *Hemilepidotus* larvae: A) *H. jordani*, 13.7 mm SL; B) *H. hemilepidotus*, 12.7 mm SL; C) *H. zapus*, 12.6 mm SL.

TABLE 1.—Comparison of some important differentiating characters in *Hemilepidotus zapus* and *H. papilio*.

Characters	This study	*H. zapus*[1]	*H. papilio*[1]
Dorsal spines	X-X1	X1 (X1-X11)	X11 (X1-X111)
Pectoral fin rays	16-17	16 (15-17)	17-18 (16-18)
Total soft fin rays; dorsal, anal, and both pectoral fins	71	67-76	69-74
Lateral line pores	54-56	52 (47-58)	59 (49-65)
Number of vertebrae	37-38	37-38	40
Number of horizontal scale rows in ventral band	ca. 8	8 or 9	ca. 4
Dorsal fin notch between third and fourth spine	yes	yes	no

[1]Data are from Peden (1978); mean is followed by range in parentheses.

larvae is *H. zapus*, while the 13.7 mm SL larva lacks urostyle pigment and is probably *H. jordani*.

Early larvae of *H. zapus* (6.5-17.0 mm SL) were linked together by the presence of melanophores above and below the urostyle (Figs. 1C, 2); such melanophores are lacking in all other known Hemilepidotinae larvae. Larvae undergoing notochord flexion can be distinguished from *H. hemilepidotus* by the lack of external pigment along the posterior body and from *H. jordani* by the presence of ventral midline pigment which curves up toward the urostyle (Fig. 1).

After notochord flexion and through the juvenile period, counts of meristic structures as well as a combination of adult characters (Peden 1978) will allow separation of the three species. Postflexion larvae of *H. zapus* have scales on the caudal peduncle that will distinguish them from other, similar-sized Hemilepidotinae larvae. These larvae also have a characteristic notch in the first dorsal fin, between the third and fourth spine, that is present in adults of all *Hemilepidotus* except *H. papilio* (Fig. 2F). A summary of some diagnostic features of all known *Hemilepidotus* larvae is presented in Table 2. Larvae and juveniles of *H. papilio* remain unknown.

General Trends of Development

Pigmentation (Fig. 2)

In the smallest larvae (6-7 mm SL), pigment appears on the head dorsally over the midbrain and on the anterior forebrain. In larger larvae 7-9 mm SL, additional pigment appears at the base of the hindbrain, posterior to the eye and in the opercular area. In postflexion larvae, head pigment increases. Separate pigment patches appear posterior to the eye (usually about 5 or 6 spots) and on the operculum dorsoposterior to the preopercular bone. Larvae 6-7 mm SL have pigment on the nape and on the dorsal surface of the gut. Gut pigment increases laterally with development, and in larger postflexion larvae it becomes more internal than external. By 14-15 mm SL, nape pigment extends ventrally to the dorsal surface of the gut.

There are five general areas of pigmentation in the postanal region: 1) an external row (appearing more or less double) of melanophores along the dorsal midline extending from the nape to the last myomere; 2) a dorsolateral row of internal pigment along the notochord, extending from the nape to about the last 4-7 myomeres; 3) an external row of melanophores along the ventral body midline from midbody (about 11 myomeres after anus) to the last myomere; 4) a ventrolateral row of internal pigment along the notochord, beginning at about 4-6 myomeres after the anus and extending to about 6 or 7 myomeres from the end of the tail; and 5) a few external melanophores along the notochord in the caudal peduncle area, and external melanophores dorsal and ventral to the notochord at the posterior tail tip. Prior to notochord flexion, at about 9.0 mm SL, the anterior ventral midline pigment gradually becomes more internal. In postflexion larvae, this ventral midline row is comprised of < 10 melanophores beginning about 17 myomeres posterior to the anus. By 16.7 mm SL, all the postanal pigment is internal except for the dorsal midline melanophores and a few spots in the caudal peduncle area. After about 17 mm SL, melanophores in the caudal peduncle are no longer visible.

Morphology (Table 3; Fig. 3)

Relative growth trends are summarized in Figure 3. Preanal length, head length, depth at pectoral fin, snout to anal fin length, and snout length increase with development. Eye diameter as a proportion of head length undergoes a gradual decrease with development. Depth at the caudal peduncle and the length from the snout to dorsal fin origin increase sharply with development in larvae about 16.0-19.0 mm SL and then decrease in larger specimens.

Meristic Structures (Tables 4, 5)

Branchiostegal rays have begun to ossify in our smallest specimens (7-8 mm SL), and the adult complement of six rays is completely ossified in larvae $\geq$ 12-13 mm SL.

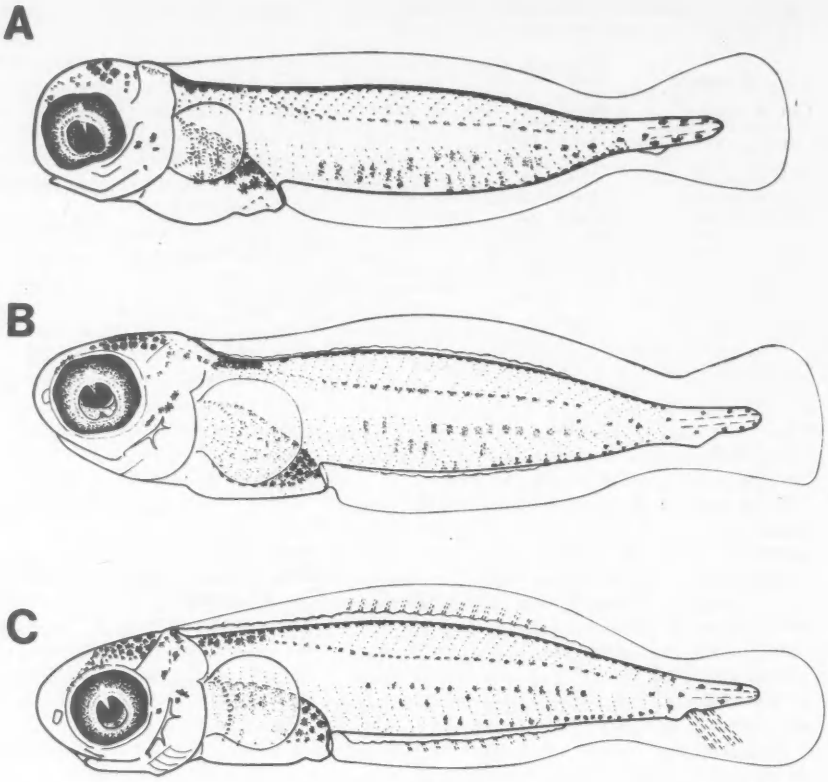

FIGURE 2.–Larvae of *Hemilepidotus zapus*: A) 6.7 mm SL; B) 8.7 mm SL; C) 11.0 mm SL;

Fins–All fin rays show their initial ossification in larvae between 12 and 13 mm SL. Fin formation occurs in the sequence: dorsal spines and fin rays, anal fin rays, and principal caudal fin rays (12-13 mm SL); pectoral fin rays (13-14 mm SL); pelvic spine and fin rays (15-16 mm SL); and secondary caudal fin rays (16-17 mm SL). The pterygiophores supporting dorsal fin rays begin ossifying at 16-17 mm SL, and those supporting anal fin rays begin ossifying at 17-18 mm SL. The largest specimen (20.0 mm SL) has completely ossified dorsal and anal pterygiophores.

Axial skeleton–Neural and haemal spines have started ossification in the smallest larvae 7-8 mm SL, and are fully ossified in larvae 15-16 mm SL. Abdominal vertebral centra are completely ossified in larvae 12-13 mm SL, but the caudal vertebral centra are not fully ossified until larvae are slightly larger at about 14-15 mm SL.

Lateral line scales do not begin ossifying until larvae are 18.0 mm SL, and our largest specimen (20.0 mm SL) has a fully ossified complement of scales.

Spination (Table 5)–The development of head spines is summarized in Table 5. The parietal and nuchal spines fuse in larvae > 13 mm SL and appear as a single spine in the larger larvae 18-20 mm SL. A postocular spine is ossified in larvae 12-13 mm SL but disappears by 18-20 mm SL. A small spine below the eye (infraorbital) ossifies by 14-15 mm SL, but is no longer visible in specimens 20 mm SL.

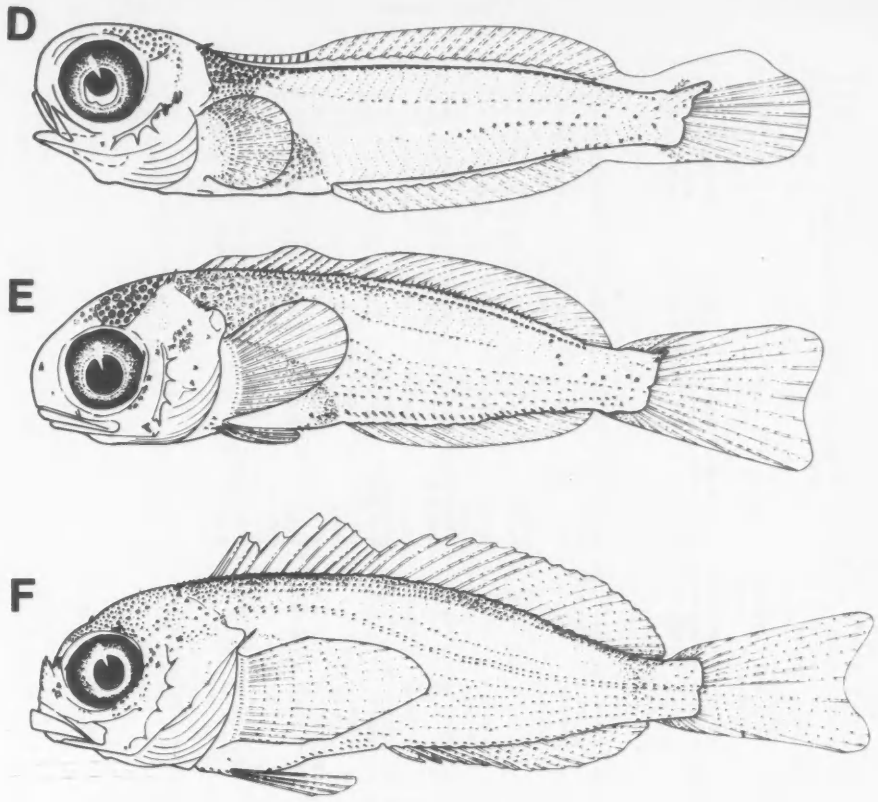

FIGURE 2.–*Continued*–D) 13.0 mm SL; E) 16.7 mm SL; F) 22.8 mm SL.

Occurrence of *Hemilepidotus zapus* in the Eastern Bering Sea

During 8 yr of sampling ichthyoplankton at a total of 250 stations in the eastern Bering Sea (in the approximate area between lat. 60°N and long. 174°W with more intensive sampling between the Pribilof Islands and Unimak Island), only 58 *Hemilepidotus zapus* larvae were collected. The number of positive stations is indicated in Figure 4.

Small *H. zapus* larvae (6.7-10.1 mm SL) were collected during winter in surface water north of the Pribilof Islands (Fig. 4A). Only a single larva (11.0 mm SL) was taken in February 1978 at the surface in about the same area over the slope (Fig. 4A). Our largest collection of larvae (12.2-16.7 mm SL) was made in late April and early May (Fig. 4B). Most of the larvae were collected in neuston nets at stations over the slope, but in May a few larvae were taken over the continental shelf. Larvae primarily occurred south of the Pribilof Islands. The largest larvae (18-22 mm SL) were collected during June and July at scattered stations throughout the area including only one northwest of the Pribilof Islands (Fig. 4C).

Although data are insufficient to document the exact time and geographical extent of spawning, the presence of small larvae indicates some spawning occurs in early winter north of the Pribilof Islands. Peden (1978) indicated that adult and postlarval *H. zapus* have been collected only along the Aleutian Islands. Further studies are needed to investigate whether larvae and juveniles move south to the Aleu-

TABLE 2.—Selected postanal pigmentation characters useful in distinguishing preflexion and flexion *Hemilepidotus* larvae.

Taxon	Pigmentation characters: Dorsal midline	Dorso-lateral	Above notochord (internal)	Below notochord (internal)	Ventro-lateral	Ventral midline	Caudal region	Diagnostic	Source
H. spinosus	By 5 mm, a continuous line from head to posteriormost myomere, becoming heavier	By 6 mm, becoming heavier	By 8-9 mm, along length of body	Not obvious	By 6 mm, becoming heavier	From anus to posterior-most myomere, >15 melanophores	Sparse, ventral midline continuous	Lateral, ventral midline	Richardson and Washington 1980
H. hemilepidotus	Until 7 mm unpigmented area between myomeres 4-11, becoming moderately heavy	By 11 mm, moderate	By 6-7 mm, along length of body	By 8-9 mm, begins posterior to anus	By 11 mm, moderate	Begins 9-10 myomeres after anus, <15 melanophores	None	Lateral, lack of caudal pigment	Richardson and Washington 1980, This study
H. jordani[1]	Similar to *H. hemilepidotus* but not as heavy	None	Similar to *H. hemilepidotus*	Similar to *H. hemilepidotus*	Some internal only	By flexion, a few internal melanophores	None	Lack of lateral and caudal pigment	This study
H. zapus	Similar to *H. hemilepidotus* but not as heavy	None	By 6 mm, along length of body	By 8 mm, incomplete, begins posterior to anus	Some internal only	Begins 11 myomeres after anus, <15 melanophores	Ventral midline continues, above and below urostyle	Urostyle	This study
H. gilberti	Pigment begins 8-9 myomeres after anus	None	None[2]	None[2]	None	Begins 10 myomeres after anus, <15 melanophores	None	Unpigmented area along dorsal midline, lack of lateral pigment	Hattori 1964

[1]Preflexion larvae of *H. hemilepidotus* and *H. jordani* cannot presently be separated.
[2]No internal pigment is shown on Hattori's figures.

TABLE 3.—Morphometrics (in millimeters) of larvae and juveniles of *Hemilepidotus zapus*. Specimens between dashed lines are undergoing notochord flexion.

Standard length	Total length	Preanal length	Head length	Snout length	Eye diameter	Depth at pectoral fin	Depth at caudal peduncle	Snout to dorsal	Snout to anal fin
6.5	6.9	2.4	1.3	0.1	0.8	1.3			
6.7	7.4	2.4	1.3	0.1	0.8	1.3			
6.7	7.2	2.4	1.3	0.1	0.8	1.3			
7.1	7.5	2.7	1.4	0.1	0.8	1.3			
7.1	7.7	2.8	1.3	0.1	0.9	1.3			
7.3	7.8	2.7	1.4	0.1	0.9	1.4			
7.6	8.2	2.7	1.3	0.1	0.9	1.4			
7.7	8.3	2.7	1.3	0.1	0.9	1.5			
8.2	8.9	3.1	1.7	0.2	1.0	1.5			
8.2	8.9	3.2	1.8	0.2	1.0	1.6			
8.5	9.1	3.3	1.9	0.3	1.0	1.6			
8.7	9.5	3.5	2.0	0.3	1.1	1.7			
8.7	9.4	3.4	2.0	0.3	1.1	1.7			
9.1	9.8	3.6	1.9	0.3	1.0	1.7			
9.2	10.0	3.6	2.1	0.2	1.1	1.7			
9.2	9.8	3.6	1.9	0.2	1.1	1.7			
9.3	10.1	3.9	2.1	0.2	1.1	1.7			
9.5	10.1	4.0	2.1	0.3	1.2	1.8			
9.8	10.5	3.6	1.9	0.2	1.1	1.7			
10.1	10.9	4.0	2.3	0.3	1.2	1.8			
11.0	12.0	4.4	2.6	0.3	1.3	2.1			
12.0	13.5	5.5	3.2	0.6	1.4	2.5	1.0	3.0	5.8
12.2	14.3	5.5	3.3	0.5	1.5	2.5	0.9		5.8
12.2	14.0	5.6	3.4	0.5	1.5	2.6	0.9	3.3	5.9
12.3	14.4	5.6	3.3	0.4	1.5	2.6	1.0	3.2	5.9
12.6	14.5	5.8	3.3	0.5	1.5	2.8	1.1	3.3	6.0
12.9	15.0	5.7	3.5	0.6	1.5	2.7	1.1	3.3	6.1
12.9	14.6	5.6	3.4	0.4	1.5	2.6	1.0	3.4	6.0
13.0	15.0	5.6	3.7	0.6	1.5	2.6	1.1	3.3	6.0
13.0	15.2	5.6	3.5	0.6	1.6	2.7	1.1	3.3	6.0
13.2	15.4	5.5	3.5	0.6	1.6	2.9	1.1	3.4	5.9
13.5	16.0	6.0	3.5	0.6	1.6	2.8	1.2	3.5	6.4
13.6	16.0	5.9	3.7	0.6	1.5	2.8	1.2	3.3	6.3
13.8	16.1	5.9	3.7	0.6	1.7	3.0	1.2	3.4	6.3
14.0	16.7	6.3	3.7	0.6	1.8	3.2	1.3	3.7	6.6
14.3	17.1	6.5	3.9	0.6	1.8	3.1	1.3	3.7	6.9
14.4	17.2	6.8	4.0	0.6	1.9	3.2	1.4	4.0	7.1
14.5	17.2	6.9	4.0	0.7	1.9	3.3	1.4	4.1	7.2
14.7	17.5	6.8	3.9	0.6	1.9	3.2	1.3	3.8	7.1
14.9	17.9	7.0	4.0	0.6	1.8	3.3	1.4	4.0	7.2
14.9	18.0	7.0	4.1	0.6	2.0	3.4	1.5	4.2	7.3
15.1	18.6	7.2	4.3	0.7	2.0	3.7	1.6	4.2	7.5
15.2	18.3	7.2	4.5	0.7	2.1	3.7	1.6	4.2	7.5
15.3	19.0	7.5	4.7	0.8	2.0	3.9	1.6	4.4	7.8
15.5	19.0	7.3	4.5	0.8	2.0	3.8	1.6	4.5	7.6
15.6	19.0	7.4	4.6	0.7	2.0	3.8	1.6	4.3	7.7
15.9	19.7	7.8	4.7	0.8	2.1	3.9	1.7	4.6	8.1
16.7	20.7	7.9	5.1	0.8	2.1	4.3	1.8	4.8	8.2
16.8	21.3	8.1	5.4	0.8	2.3	4.5	1.7	5.1	8.5
16.9	20.9	8.2	5.2	0.8	2.2	4.4	1.7	5.0	8.6
18.0	23.0	9.0	6.2	1.0	2.3	5.5	1.9	5.2	9.3
19.1	25.0	9.8	6.3	1.0	2.3	5.6	2.0	5.4	10.0
19.3	24.9	10.1	7.0	1.3	2.6	5.7	1.9	6.1	10.5
20.5	26.0	10.5	6.7	1.3	2.5	6.2	2.0	5.5	10.9
21.0	26.5	10.9	7.0	1.3	2.5	6.3	2.1	5.7	11.1
21.0	26.6	11.1	7.0	1.5	2.5	6.3	2.0	6.0	11.5
21.2	27.0	11.4	7.2	1.6	2.5	6.5	2.0	6.1	11.6
22.0	27.5	11.5	7.3	1.3	2.6	6.7	2.1	6.0	11.9

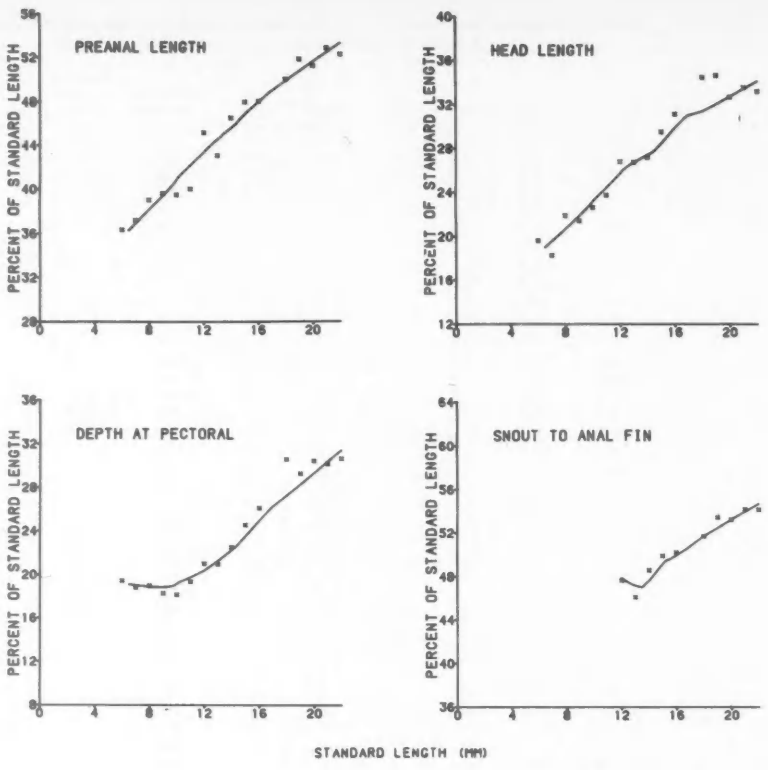

FIGURE 3.—Relative trends in selected morphometric features

TABLE 4.—Development of meristic characters in larvae of *Hemilepidotus*

Size interval (mm SL)	Sample size	Fin rays						
						Caudal		
		Dorsal	Anal	Pectoral	Pelvic	Principal	Secondary	Total
7-8	2							
8-9	3							
9-10	2							
[1]10-12	—							
12-13	3	X,11-21	17	8-10	I,0	12	3-5	15-17
13-14	1	XI,21	17	16	I,3	12	9	21
14-15	3	X-XI-20-21	17	13-16	I,3	12	9	21
15-16	2	X,21	17	16	I,4	12	11-13	23-25
16-17	1	XI,20	17	17	I,4	12	15	27
18	1	XI,20	16	16	I,4	12	15	27
20	1	XI,21	17	16	I,4	12	14	26

[1]Specimens in this size group did not accept alizarin stain.
[2]Haemal spines 23-24 are fused.

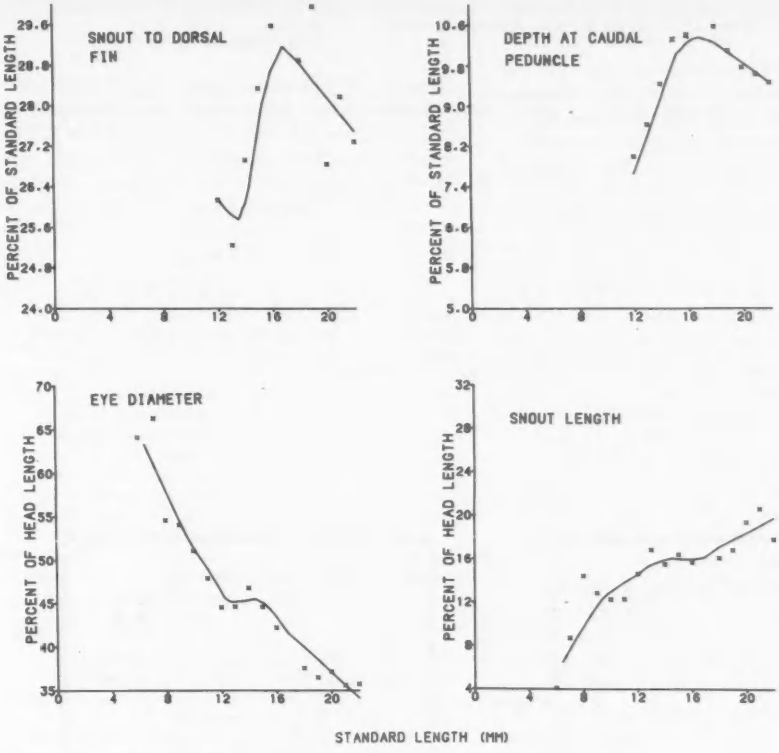

FIGURE 3. –*Continued*– during ontogeny in *Hemilepidotus zapus*.

zapus. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Pterygiophores		Axial skeleton				Branchiostegal rays	Lateral line scales
				Spines		Centra			
		Dorsal	Anal	Neural	Haemal	Precaudal	Caudal		
7-8	2			12-19	9			2-3	
8-9	3			20	10			4	
9-10	2			29	17			5	
[1]10-12	—								
12-13	3			35	22	12	23	6	
13-14	1			36	23	12	25	6	
14-15	3			36	24	12	24-26	6	
15-16	2			37	[2]25	12	26	6	
16-17	1	15		37	24	12	25	6	
18	1	30	16	37	25	12	26	6	54
20	1	31	17	37	24	12	26	6	56

TABLE 5.—Development of spines in the head region of *Hemilepidotus zapus* larvae. Specimens below the dashed line have completed notochord flexion.

Size interval (mm SL)	Sample size	Parietal	Nuchal	Preopercular	Opercular	Postocular	Superior infraorbital	Nasal	Articular	Cleithral	Posttemporal supracleithral
7-8	2	0-1		2							
8-9	3	1		3							
9-10	2	1		3							
[1]10-12											
12-13	3	[2]1		[2]1	4		1			1		1-2
13-14	1	[2]1		[2]1	4		1		1	1		2
14-15	3	[2]1		[2]1	4	3	1	1	1	1		2
15-16	2	[2]1		[2]1	4	3	1	1	1	1		[3]3
16-17	1	[2]1		[2]1	4	3	1	1	1	1	1	[3]3
18	1		1		4	3	0	1	1	1	1	[3]3
20	1		1		4	3	0	0	1	[3]1	1	[3]3

[1]Specimens in this size group did not accept alizarin stain.
[2]Spines are beginning to fuse at base but points can still be observed.
[3]Spine(s) reduced in size.

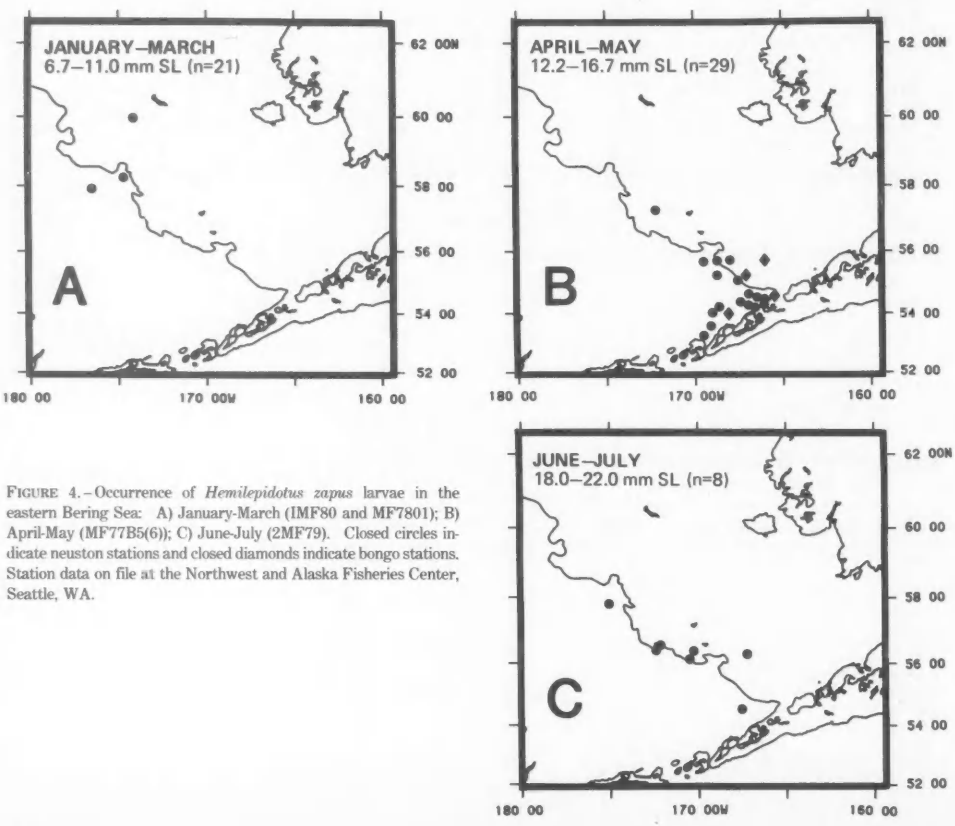

FIGURE 4.—Occurrence of *Hemilepidotus zapus* larvae in the eastern Bering Sea: A) January-March (IMF80 and MF7801); B) April-May (MF77B5(6)); C) June-July (2MF79). Closed circles indicate neuston stations and closed diamonds indicate bongo stations. Station data on file at the Northwest and Alaska Fisheries Center, Seattle, WA.

tians or whether adult *H. zapus* range further north.

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We thank Jean R. Dunn and Arthur W. Kendall, Jr. (Northwest and Alaska Fisheries Center) for helpful discussions and review of the manuscript. Alex E. Peden (British Columbia Provincial Museum) kindly assisted in the identification of *Hemilepidotus zapus* postflexion larvae.

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ANN C. MATARESE
BEVERLY M. VINTER

NOAA, National Marine Fisheries Service
Northwest and Alaska Fisheries Center
2725 Montlake Boulevard East
Seattle, WA 98112-2097

AN APPROACH TO ESTIMATING AN ECOSYSTEM BOX MODEL

Recent trends in ecosystem modeling have produced complex simulation models which are very data intensive (Andersen and Ursin 1977; Laevastu and Larkins 1981). However, in many situations the construction of a biomass budget for a box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982; Polovina 1984).

The ECOPATH model is an analytical procedure to estimate a biomass budget for a box model of an ecosystem given inputs which specify the components of the ecosystem, together with their mortality, diet, and energetics value. A computer program for ECOPATH has been written in BASIC-80, version 5.21, by Microsoft[1] (CP/M version). A listing of the ECOPATH computer program and a user's manual are available from the author.

The ECOPATH model produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the user specified species-groups. The species-groups represent aggregations of species with similar diet and life history characteristics and which have a common physical habitat. The ECOPATH model is not a simulation model with a time component as are some more complex ecosystem models. It estimates a biomass budget for the marine ecosystem in a static situation under the assumption that the ecosystem is at equilibrium conditions.

Equilibrium conditions are defined to exist when the mean annual biomass for each species-group does not change from year to year. This condition results in a system of biomass budget equations which, for species-group i, can be expressed as

> Production of biomass for species i – all predation on species i – nonpredatory biomass mortality for species i – fishery catch for species i = 0 for all i. (1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i's. The mean annual biomass estimates are obtained by solving the system of simultaneous linear equations.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The formulation of each term of the biomass budget equation will now be presented in detail.

The Model

Biomass Production

Production (P) for a cohort of animals over 1 yr is defined as

$$P = \int_0^1 N_t \frac{d}{dt}(w_t)\, dt$$

and mean annual biomass (B) for the cohort is defined as

$$B = \int_0^1 N_t\, w_t\, dt$$

where N_t is the number of animals and w_t the mean individual weight at time t.

Allen (1971) investigated the production to biomass (P/B) ratio for a cohort over a range of mortality and growth functions. For a number of growth and mortality functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species-group which consists of n cohorts or species, with instantaneous annual total mortality (Z_i) for cohort or species i, where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species-group production (P) is the sum of the cohort production (P_i) and can be expresed as

$$P = \sum_{i=1}^{n} P_i = \sum_{i=1}^{n} Z_i B_i. \qquad (2)$$

Under the assumption that the Z_i's are all equal to say Z, then total species-group production can be expressed as

$$P = Z \cdot B$$

where B is the mean annual species-group biomass.

Allen (1971) has also shown that when growth in weight is linear, the P/B ratio is equal to the reciprocal of the mean age for a range of mortality functions. For a number of other growth and mortality functions the ratio of cohort P/B can be the reciprocal of the mean lifespan. Thus, for a range of growth and mortality functions, total species-group production can be expressed as

$$P = C \cdot B$$

where B is the mean annual species-group biomass, and C is a parameter.

In an application of ECOPATH to an ecosystem of French Frigate Shoals where there was very little fishing mortality, the P/B ratio for fishes and crustaceans was taken as the annual instantaneous natural mortality (M); whereas, for primary and secondary producers whose growth is more likely to be linear than the von Bertalanffy, the P/B ratio was estimated as the reciprocal of the mean age (Polovina 1984).

Predation Mortality

The predation mortality is the fraction of the biomass of a species-group which is consumed by all predators excluding fishing mortality. Two types of information are needed. First the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i. The primary source of this information is the analysis of stomach contents data. At least in one study it has been shown that there is a high correlation between diet indices based on weight, volume, and percentage of occurrence for stomach content data, and thus either index may be used to generate the DC matrix (Macdonald and Green 1983). The second type of information needed to ascertain predation mortality is the food requirements of the predator. The ECOPATH model requires the user to specify FR_i, the ratio of annual consumption to mean annual biomass. The annual food required by the predator is the product of FR_i and B_i.

Some values of daily food required as a fraction of body weight range from 0.005 to 0.02 (Laevastu and Larkins 1981). Based on these daily estimates a range of annual food required as a fraction of mean biomass (FR_i) is 1.8 to 7.3.

Nonpredation Mortality

All mortality attributable to causes other than predation and fishing is termed nonpredatory mortality. The ECOPATH model defines ecotrophic efficiency e_i as the fraction of total production which is removed by fishing and predation mortality. This

was 0.95 in the French Frigate Shoals model. The nonpredator mortality rate is $(1 - e_i) \cdot Z_i$, and the amount of production which goes to nonpredation mortality is

$$(1 - e_i) P_i = (1 - e_i) C_i B_i.$$

For n species-groups the biomass budget Equation (1) becomes a system of n simultaneous equations as follows:

$$C_1 B_1 - \sum_{k=1}^{n} (FR_k) B_k DC_{k1} - (1 - e_1) C_1 B_1 = \text{catch}_1,$$

$$\vdots$$

$$C_i B_i - \sum_{k=1} (\text{FR}_k) B_k DC_{ki} - (1 - e_i) C_i B_i = \text{catch}_i,$$

$$\vdots$$

$$C_n B_n - \sum_{k=1}^{n} (FR_k) B_k DC_{kn} - (1 - e_n) C_n B_n = \text{catch}_n.$$

With input estimates for parameters C_i, FR_i, DC_{ij}, and e_i for all i and j, and catches (catch_i) if there is fishing, this system of equations is a system of n simultaneous equations linear in the unknown B_i's. This system of equations can be expressed in matrix form as $AB = C$, where A is an $n \times n$ matrix of coefficients, B is an n-dimensional vector of mean annual species group biomass, and C is the vector of fishery catch where the ith element is the total catch of the ith species-group.

If the matrix A is of full rank and if there are some fishery catches for some species so the vector C is not null, then there typically exists a unique nontrivial solution vector of biomass B. If there are no fishery catches then it is necessary to provide an estimate of at least one of the mean species group biomass B_i before there exists a unique nontrivial biomass vector B which solves the budget equation. In the application of ECOPATH to an ecosystem at French Frigate Schoals where there was no fishing mortality, the biomasses of three apex predators were estimated from field censuses and treated as known inputs. In this application the ith element of C vector was the annual predation by the three apex predators on the ith species-group.

Five years of field work targeting most of the components of the marine ecosystem at French Frigate Schoals in the Northwestern Hawaiian Islands provided the estimates for many of the input parameters required by the ECOPATH model as well as some estimates of biomass and production to serve to evaluate the estimates produced by the model. The estimates of biomass and production generated by the application of ECOPATH to French Frigate Shoals are given in Figure 1. In general the model's estimates of biomass and production are in good agreement with the available field data (Polovina 1984). In the application of the French Frigate Shoals, the biomasses of the top level carnivores are treated as fixed inputs thus a particularly appropriate validation of the model is the comparison of the estimate of net benthic primary production with an independent estimate from field data. The model estimated net benthic primary production, adjusted to the total 1,200 km^2 habitat of French Frigate Shoals, at 2.3×10^6 kg $\cdot$ $km^{-2} \cdot yr^{-1}$ while the estimate based on field data was 2.5×10^6 kg $\cdot$ $km^{-2} \cdot yr^{-1}$ (Grigg et al. 1984).

The Computer Program

The ECOPATH model has been implemented via two BASIC language programs. The "dialect" of the language used is BASIC-80, version 5.21, by Microsoft (CP/M version). These programs are designed to be used interactively on a terminal or a hard-copy printer. The first program is the input parameter program which accepts the input parameters and formats them into a BASIC sequential file. The second program is the ECOPATH model itself.

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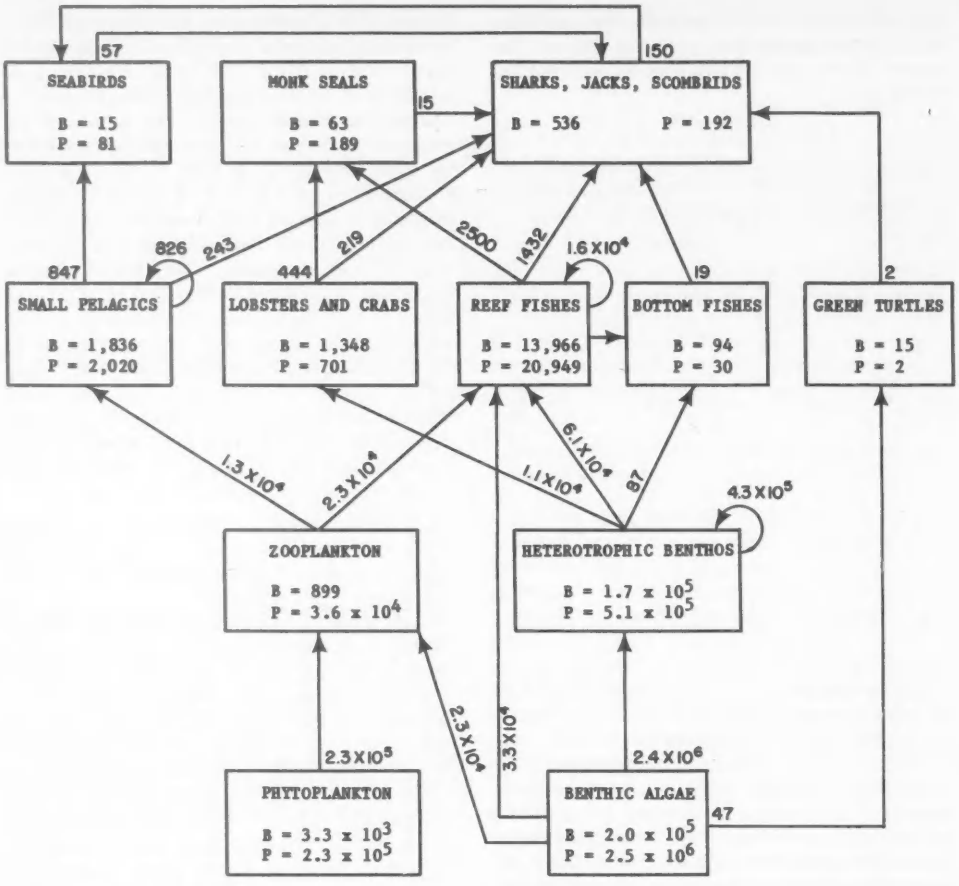

FIGURE 1.—Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of (kg/km)^2 based on a habitat area of 1,200 km^2. The values associated with the arrows represent the production from the lower trophic level consumed by the higher trophic level (Polovina in press).

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JEFFREY J. POLOVINA
MARK D. OW

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830
Honolulu, HI 96812

FOOD AND FEEDING OF THE TOMTATE, *HAEMULON AUROLINEATUM* (PISCES, HAEMULIDAE), IN THE SOUTH ATLANTIC BIGHT[1]

The tomtate, *Haemulon aurolineatum*, is an abundant demersal fish in a variety of marine habitats in the South Atlantic Bight, the Gulf of Mexico, and the Caribbean Sea (Darcy 1983). They are a reef-associated species (Parrish and Zimmerman 1977), and in the South Atlantic Bight they are most commonly found over hard or "live" bottom reefs in depths < 55 m (Struhsaker 1969; Manooch and Barans 1982; Sedberry and Van Dolah 1984). While occasionally taken in trawl catches over open, sandy habitats on the southeastern continental shelf (Wenner et al. 1980), they are much more abundant in trawls directed at sampling hard bottom, and generally rank in the top three demersal species by number or weight in trawl catches (Wenner 1983; Sedberry and Van Dolah 1984; Sedberry unpubl. data). Although they are frequently caught on hard bottom reefs in the South Atlantic Bight, the dependance of these fishes on hard bottom habitat for food is unknown. Previous investigations in the Caribbean have indicated that tomtate are not obligatory reef dwellers and that they forage extensively in open sandy areas (see Darcy 1983 for review). Because of the importance of this species in the hard bottom ichthyofauna of the South Atlantic Bight and its importance to fisheries associated with hard bottom reefs, a knowledge of its food habits is important to our understanding the ecology of this habitat. Tomtate may be important in transferring energy from the expansive sand areas of the shelf onto the much more restricted hard bottom habitat, and their feeding behavior in the South Atlantic Bight may be important in maintaining the higher biological productivity of hard bottom areas, relative to the open sandy shelf.

To determine foraging habitat of the tomtate, an investigation on food habits was conducted. The purpose of this note is to report the results of that study and to relate the feeding behavior to existing knowledge of the ecology of hard bottom areas in the South Atlantic Bight.

Methods

Tomtate were collected during seasonal cruises in 1980 (two cruises – one in winter and one in summer) and 1981 (four cruises – one each in winter, spring, summer, and fall) by trawl from eight hard bottom reef stations off South Carolina and Georgia. Stations were located in each of three depth zones representing the inner shelf (16-22 m depth, three stations), middle shelf (23-38 m, four stations), and the outer shelf (47-67 m, one station). Detailed descriptions of station locations and habitat can be found in Sedberry and Van Dolah (1984) and Wenner et al. (1984). Each station was mapped using loran C and underwater television, and all sampling was conducted in hard bottom areas mapped by using this technique (Sedberry and Van Dolah 1984).

Tomtate were measured (standard length, SL) at sea and their stomachs removed if not conspicuously empty. Stomachs were individually labeled and preserved in 10% seawater-Formalin[2].

Stomachs were washed in tap water and transferred to 50% isopropanol in the laboratory, and contents of individual stomachs were sorted by taxa and counted. Colonial forms (e.g., hydroids, bryozoans) and algae were counted as one organism. Volume displacement of food items was measured using a graduated cylinder, or estimated by using a 0.1 cm^2 grid (Windell 1971).

Since the methods of food habits quantification are variously biased (Hynes 1950; Pinkas et al. 1971; Windell 1971), the relative contribution of different food items to the total diet was determined using three methods: 1) percent frequency occurrence (F), 2) percent numerical abundance (N), and 3) percent volume displacement (V). These three values were calculated for individual prey species, for prey grouped by higher taxonomic categories, and for higher taxonomic categories pooled for 100 mm intervals of standard length. To determine the dependance of tomtate on hard bottom prey organisms, stomach samples were compared with benthic samples using Ivlev's index of electivity (Ivlev 1961), calculated as follows:

$$E = \frac{P_1 - P_2}{P_1 + P_2}$$

where P_1 is the percentage of the diet comprised by a given prey taxon and P_2 is the percentage of the food complex in the environment (i.e., in benthic samples) comprised by the same prey taxon. Electivity values range from -1 to $+1$. Negative values imply that the prey species is avoided by the predator or that it

[1]Contribution No. 179, South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species which occur in a different habitat than those sampled by the benthic sampler. A value near zero implies no selectivity by the predator; i.e., the fish is feeding on the prey in proportion to the prey's relative abundance.

Benthic samples and stomach collections were pooled by depth zone (inner, middle, and outer shelf) for comparison; however, too few tomtate for adequate comparison were collected at outer shelf stations. Benthic samples were obtained with diver-operated suction sampler at the seven inner and middle shelf, hard bottom sites during the same time periods in 1980 and 1981 as the fish collections were made. The suction sampler is very effective at sampling macroinvertebrates on hard substrates (Chess 1979; Wenner et al. 1983). Five replicate benthic samples were taken during the six cruises at each reef that was sampled for fishes, and these samples (30 for each reef) are believed to be adquate representatives of the hard bottom invertebrate fauna in

TABLE 1.—Percent frequency occurrence (F), percent number (N), and percent volume (V) of food items in *Haemulon aurolineatum* stomachs collected at hard bottom areas in 1980 and 1981.

Taxon	Food item	F	N	V
Algae				
	Sargassum sp.	1.0	0.1	0.1
Cnidaria				
	Hydrozoa			
	Dynamena cornicina	1.0	0.1	<0.1
	Lictorella convallaria	1.0	0.1	<0.1
	Sertularia sp.	1.0	0.1	<0.1
	Total Hydrozoa	3.2	0.2	<0.1
	Anthozoa			
	Actiniaria undetermined	5.3	0.4	0.6
Platyhelminthes				
	Turbellaria undetermined	5.3	1.0	0.7
Annelida				
	Polychaeta			
	Ampharete sp.	1.0	0.1	<0.1
	Amphinomidae undetermined	1.0	0.1	<0.1
	Arabella iricolor	2.1	0.2	0.5
	Arabellidae undetermined	1.0	0.1	0.1
	Armandia maculata	6.3	2.4	0.3
	Capitellidae undetermined	5.3	0.4	0.4
	Ceratonereis mirabilis	1.0	0.1	<0.1
	Chloeia sp.	1.0	0.1	0.2
	Chloeia viridis	1.0	0.1	0.4
	Chone americana	2.1	0.2	<0.1
	Diopatra cuprea	1.0	0.1	<0.1
	Drilonereis sp.	2.1	0.2	0.1
	Eunice vittata	1.0	0.1	<0.1
	Eunice websteri	1.0	0.1	<0.1
	Eunicidae undetermined	1.0	0.1	<0.1
	Exogone dispar	2.1	0.2	<0.1
	Glycera sp.	5.3	0.4	1.2
	Glycera americana	3.2	0.2	0.8
	Glycera tesselata	2.1	0.2	0.3
	Goniadides carolinae	1.0	0.1	<0.1
	Harmothoe sp.	2.1	0.2	<0.1
	Lumbrinerides acuta	1.0	0.1	<0.1
	Lumbrineris coccinea	2.1	0.2	0.9
	Lumbrineris sp.	1.0	0.1	0.9
	Malanidae undetermined	3.2	0.5	0.2
	Nephtyidae undetermined	1.0	0.1	<0.1
	Nephtys incisa	1.0	0.1	<0.1
	Notomastus americanus	1.0	0.1	<0.1
	Notopygos crinita	1.0	0.1	0.1
	Onuphis sp.	1.0	0.1	<0.1
	Onuphis eremita	1.0	0.1	<0.1
	Onuphis nebulosa	1.0	0.1	0.4
	Opheliidae undetermined	1.0	0.1	<0.1
	Phyllodoce castanea	1.0	0.1	<0.1
	Phyllodoce groenlandica	1.0	0.1	0.1
	Phyllodoce longipes	1.0	0.2	<0.1
	Phyllodoce sp.	1.0	0.1	<0.1
	Phyllodocidae undetermined	1.0	0.1	<0.1
	Polychaeta undetermined	5.3	0.4	3.1
	Progoniada regularis	1.0	0.1	<0.1
	Psalmmolyce ctenidophora	2.1	0.2	1.5
	Sabellidae undetermined	1.0	0.1	0.2
	Scoloplos rubra	1.0	0.1	0.2
	Sphaerodoridae undetermined	1.0	0.1	<0.1
	Syllidae undetermined	2.1	0.2	<0.1
	Syllis sp.	3.2	0.2	0.1
	Syllis regulata carolinae	1.0	0.1	<0.1
	Terebellidae undetermined	2.1	0.2	2.0
	Travisia parva	1.1	0.2	0.1
	Total Polychaeta	46.3	8.7	14.6
Mollusca				
	Gastropoda			
	Caecum pulchellum	1.0	0.1	<0.1
	Diodora cayenensis	1.0	0.1	<0.1
	Gastropoda undetermined	1.0	0.1	0.4
	Naticidae undetermined	1.0	0.1	<0.1
	Total Gastropoda	3.2	0.3	0.5
	Pelecypoda			
	Ervilia concentrica	5.3	38.2	6.3
	Mactra fragilis	1.0	0.1	0.2
	Pelecypoda larvae	1.0	0.1	<0.1
	Total Pelecypoda	7.4	38.3	6.5
	Cephalopoda			
	Octopus sp.	1.0	0.1	0.9
Pycnogonida				
	Anoplodactylus insigniformis	1.0	0.1	<0.1
Crustacea				
	Copepoda			
	Calanopia americana	5.3	13.0	0.3
	Longipedia helgolandica	2.1	0.6	<0.1
	Microsetella norvegica	1.0	0.2	<0.1
	Saphirella tropica	1.0	0.1	<0.1
	Temora stylifera	3.2	0.4	<0.1
	Temora turbinata	6.3	1.2	<0.1
	Undinula vulgaris	1.0	0.1	<0.1
	Total Copepoda	13.7	15.4	0.4
	Stomatopoda			
	Gonodactylus bredini	2.1	0.2	1.4
	Lysiosquilla scabricauda	1.0	0.1	1.7
	Stomatopoda larvae	3.2	0.3	0.3
	Stomatopoda undetermined	4.2	0.3	0.4
	Total Stomatopoda	10.5	0.8	3.8
	Mysidacea			
	Bowmaniella portoricensis	3.2	0.2	0.1
	Cumacea			
	Cumacea B	1.0	0.1	<0.1
	Oxyurostylis smithi	3.2	0.2	<0.1
	Total Cumacea	4.2	0.3	<0.1

each depth zone (Wenner et al. 1983, 1984). Details of benthic sampling and structure of the invertebrate communities are described elsewhere (Wenner et al. 1983, 1984). The electivity index was calculated for each species that were numerically dominant in fish stomachs or in benthic samples collected within the two depth zones (inner and middle shelf).

Results and Discussion

Haemulon aurolineatum had a generalized diet and fed on about 120 species of prey (Table 1). Polychaetes and amphipods were the most important food and were eaten with almost the same frequency. Polychaetes, however, made up a large volume of prey because of their large size. Decapods were also frequently consumed, but made up a small percentage of the volume or number of prey items. Pelecypods were the most abundant prey and cephalochordates, while infrequently consumed, made up a large portion of food volume because of their large size. Fishes also made up a large portion of food volume and copepods, though small in volume displacement, were often eaten in large numbers.

TABLE 1.—*Continued.*

Taxon / Food item	F	N	V
Tanaidacea			
Apseudes sp. B	1.0	0.7	<0.1
Isopoda			
Carpias bermudensis	1.0	0.1	<0.1
Erichsonella filiformis	1.0	0.1	<0.1
Eurydice littoralis	3.2	0.2	0.1
Paracerceis caudata	1.0	0.1	<0.1
Total Isopoda	6.3	0.4	0.1
Amphipoda			
Acanthonotozomatidae	1.0	0.1	<0.1
Ampelisca sp.	1.0	0.1	<0.1
Ampelisca cristoides	1.0	0.1	0.1
Ampelisca schellenbergi	3.2	0.3	0.1
Ampelisca vadorum	1.0	0.1	0.1
Amphipoda E	3.1	0.2	<0.1
Amphipoda G	1.0	0.2	<0.1
Amphipoda undetermined	2.1	0.2	0.1
Caprella equilibra	13.7	1.7	0.2
Caprella penantis	3.2	0.4	0.1
Cerapus tubularis	1.0	0.1	<0.1
Elasmopus sp. A	2.1	0.4	<0.1
Elasmopus sp.	1.0	0.1	<0.1
Erichthonius brasiliensis	12.6	2.1	0.2
Gammaropsis sp.	2.1	0.4	<0.1
Lembos unicornis	1.0	0.1	<0.1
Leucothoe spinicarpa	1.0	0.1	<0.1
Liljeborgia sp. A	2.1	0.2	<0.1
Luconacia incerta	2.1	1.5	0.1
Lysianopsis alba	4.2	0.7	0.1
Melita appendiculata	2.1	1.0	0.1
Metharpinia floridana	1.0	0.2	<0.1
Microjassa sp. A	1.0	0.2	<0.1
Monoculodes sp.	1.0	0.1	<0.1
Photis sp.	3.1	0.4	<0.1
Photis pugnator	1.0	0.2	<0.1
Phtisica marina	2.1	0.3	<0.1
Rhepoxynius epistomus	2.1	0.2	<0.1
Rudilemboides naglei	6.3	0.7	<0.1
Stenopleustes sp. A	1.0	0.1	<0.1
Stenothoe sp.	3.2	0.2	<0.1
Stenothoe georgiana	5.3	0.8	<0.1
Synchelidium americanum	1.0	0.1	<0.1
Tiron tropakis	1.0	0.1	<0.1
Total Amphipoda	47.4	12.8	1.3
Decapoda			
Albunea paretii zoea	1.0	0.1	<0.1
Alpheus normani	1.0	0.1	<0.1
Brachyura megalopae	1.0	1.2	0.1
Brachyura undetermined	2.1	0.2	0.3
Callianassa atlantica	1.0	0.1	0.9
Decapoda larvae	1.0	0.1	<0.1
Leptochela sp.	1.0	0.1	0.4
Leptochela papulata	7.4	0.7	1.7
Lucifer faxoni	3.2	0.4	<0.1
Lysmata sp.	1.0	0.2	<0.1
Natantia undetermined	4.2	0.4	0.6
Neopontonides beaufortensis	1.0	0.1	<0.1
Paguridae	1.0	0.1	<0.1
Periclimenaeus schmitti	1.0	0.1	<0.1
Periclimenes sp.	1.0	0.1	0.1
Periclimenes longicaudatus	2.1	0.2	0.1
Processa sp.	4.2	0.3	0.9
Processa hemphilli	1.0	0.1	0.2
Synalpheus minus	1.0	0.1	0.1
Synalpheus townsendi	1.0	0.1	<0.1
Thor sp.	1.0	0.1	0.2
Thor floridanus	1.0	0.1	<0.1
Trachypenaeus constrictus	2.1	0.2	0.1
Xanthidae	1.0	0.1	0.2
Total Decapoda	33.7	4.9	6.2
Sipunculida			
Sipunculida D	1.0	0.1	<0.1
Bryozoa			
Amathia distans	1.0	0.1	<0.1
Crisia sp.	1.0	0.1	<0.1
Diaperoecia floridana	2.1	0.2	<0.1
Discoporella umbellata	1.0	0.1	<0.1
Total Bryozoa	5.3	0.4	0.1
Echinodermata			
Echinoidea			
Clypeasteroidea undetermined	1.0	0.7	<0.1
Ophiuroidea			
Hemipholis elongata	1.0	0.1	<0.1
Ophiothrix angulata	3.2	0.4	0.4
Ophiuroidea undetermined	17.9	1.5	1.5
Total Ophiuroidea	22.1	1.9	1.9
Chaetognatha			
Chaetognatha undetermined	1.0	0.1	<0.1
Chordata			
Cephalochordata			
Branchiostoma caribaeum	4.2	12.4	41.6
Pisces			
Bothidae undetermined	1.0	0.1	0.2
Clupeidae undetermined	1.0	0.1	1.0
Hypleurochilus geminatus	1.0	0.1	0.4
Teleostei larvae	1.0	0.1	<0.1
Teleostei undetermined	10.5	0.7	18.8
Total Pisces	14.7	1.0	20.5
Number of stomachs examined:	154		
Examined stomachs with food:	95		

Ophiuroids were frequently consumed but were usually represented in stomachs by small arm fragments.

Small (1-100 mm SL) tomtate had a diet dominated numerically by very small crustaceans (copepods) and volumetrically by fishes and decapods (Table 2). Amphipods were most abundant prey taxon for 101-150 mm tomtate and polychaetes made up the greatest volume of food. Large (151-200 mm SL) tomtate primarily consumed pelecypods, which were the most abundant taxon, and cephalochordates, which were abundant in the diet and made up the greatest prey volume.

Many hard bottom invertebrates that were abundant in suction samples at inner and middle shelf sites were not important in the diet of tomtate (Table 3). Of the eight dominant hard bottom invertebrate species, only two (the polychaete *Chone americana* and the corophoid amphipod *Erichthonius brasiliensis*) at inner shelf sites and one (the caprellid amphipod *Luconacia incerta*) at middle shelf sites made up a greater percentage of the diet than they did of benthic samples. On the other hand, invertebrates that were common in stomachs were generally not abundant in benthic samples and electivity values were usually positive.

Tomtate are apparently not completely dependent on hard bottom habitat for prey. Some of the most abundant prey species are pelagic (e.g., brachyuran megalopae, copepods). Most benthic prey are infaunal species that are restricted to soft sediments. *Armandia maculata*, a dominant prey species on the inner shelf, is a deposit-feeding polychaete that burrows in soft sediments (Fauchald and Jumars 1979). *Ervilia concentrica*, an important prey species on the middle shelf, was not collected at any of the 11 hard bottom stations. This bivalve is common in soft sediments (Porter 1974). The cephalochordate *Branchiostoma caribaeum*, a common prey species on the middle shelf that was very rare in benthic samples, is also an infaunal sand bottom species (Hildebrand and Schroeder 1928). Thus, a large portion of the prey of *Haemulon aurolineatum* are not hard bottom epifaunal species, suggesting that tomtate are not

TABLE 2.—Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of *Haemulon aurolineatum*, by length interval.

	Length Intervals (mm SL)								
	1-100			101-150			151-200		
Prey taxon	F	N	V	F	N	V	F	N	V
Algae	4.8	0.4	2.6						
Cnidaria									
Hydrozoa							6.2	0.3	<0.1
Anthozoa				8.3	1.1	3.0	6.3	0.3	0.4
Turbellaria				12.5	4.0	6.3	4.2	0.7	0.1
Annelida	19.0	1.5	11.4	62.5	15.6	35.9	50.0	9.4	13.5
Mollusca									
Gastropoda				8.3	1.1	4.7	2.1	0.2	<0.1
Pelecypoda				4.1	0.6	<0.1	12.5	57.2	8.0
Cephalopoda							2.1	0.1	1.1
Arthropoda									
Pycnogonida				4.2	0.6	0.1			
Copepoda	47.6	77.1	14.4	4.2	0.6	<0.1	4.2	0.3	<0.1
Stomatopoda	19.0	1.9	14.7	12.5	1.7	2.2	6.2	0.3	4.0
Mysidacea							6.2	0.3	0.1
Cumacea	4.8	0.4	0.2				6.2	0.3	<0.1
Tanaidacea				4.2	0.6	<0.1			
Isopoda				12.5	1.7	0.1	6.2	0.3	0.2
Amphipoda	33.3	6.0	7.3	79.2	58.3	7.7	39.6	5.9	0.5
Decapoda	19.0	9.8	20.8	33.3	5.6	11.3	39.6	3.2	5.6
Sipunculida	4.8	0.4	0.7						
Bryozoa				8.3	1.1	0.4	6.2	0.3	<0.1
Echinodermata									
Echinoidea							2.1	0.1	<0.1
Ophiuroidea	14.3	1.1	1.7	25.0	5.0	8.0	22.9	1.4	1.0
Chaetognatha	4.8	0.4	0.4						
Chordata									
Cephalochordata				4.2	0.6	2.4	6.2	18.4	51.1
Pisces	4.3	1.1	26.0	16.7	2.2	17.8	12.5	0.7	14.1
Number of stomachs examined:		28			44			79	
Examined stomachs with food:		21			24			48	
Mean length of fish with food (mm SL):		71.5			138.2			168.3	
Length extremes in interval (mm SL):		49-99			101-150			151-198	

restricted to hard bottom habitat for food resources. Although numerous in hard bottom areas (it ranked third in total number and second in total weight in trawl catches over all eight trawlable stations and six sampling periods combined in 1980 and 1981), *Haemulon aurolineatum* has been characterized as a reef-related species; i.e., it uses the reef for only part of each day (Parrish and Zimmerman 1977). Randall (1967) found sand-dwelling organisms in 16 tomtate stomachs he examined, but the habitat of the decapods, the predominant prey, could not be inferred from his results. Parrish and Zimmerman (1977) noted a diet dominated by sand-flat invertebrates for an unspecified number of tomtate collected in the Caribbean. Parrish and Zimmerman (1977) reported nocturnal foraging, with tomtate sheltering in the reef during the day. During extensive (about 70 dives) daytime scuba observations by the author off of South Carolina and Georgia, no tomtate that exhibited foraging behavior was seen, and large schools were often noted "stacked up" at the edge of rock ledges protruding out into sand areas. Apparently, nocturnal feeding behavior described for tomtate in the Caribbean is also typical for the species in the South Atlantic Bight. Tomtate forage, apparently at night, on sand bottom areas of the shelf or in sand patches often found adjacent to rock outcrops, returning to the reefs for shelter during the day. This behavior probably results in considerable energy transfer, in the form of feces, from open sand bottom areas of the shelf onto hard bottom reefs.

The fact that two hard bottom invertebrate species (*Erichthonius brasiliensis* and *Luconacia incerta*) were common in tomtate stomachs and that many additional hard bottom species (e.g., hydroids, many amphipods, alpheid decapods, and bryozoans) are occasionally eaten indicates that tomtate also forage to a limited extent on hard bottom.

The high diversity found in hard bottom invertebrate communities (Wenner et al. 1983) could be attributed, in part, to predation by abundant and diverse fish communities (Petersen 1979). However, as noted by Wenner et al. (1983), available data indicate that few dominant species of hard bottom invertebrates are heavily preyed upon by fishes (Sedberry and Nimmich[3]). Tomtate, an abundant

[3]Sedberry, G. R., and T. A. Nimmich. Food habits of some fishes associated with live bottom habitat off the South Atlantic coast of the U.S.A. Manuscr. in prep. South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412.

TABLE 3.—Relative abundance (percent of total number of individuals) and electivity index values (*E*) of dominant species in suction samples (Group A) and *Haemulon aurolineatum* stomachs (Group B) by depth zone. Dominant species included those that ranked in the five most abundant species within each Group (A or B) in either depth zone, for collections pooled for all years and seasons.

	Percent of total number of individuals					
	Inner shelf			Middle shelf		
	Benthic samples	Fish stomachs	*E*	Benthic samples	Fish stomachs	*E*
Group A:						
Chone americana	0.33	0.36	0.04	0.81	0.09	−0.79
Erichthonius brasiliensis	2.89	9.32	0.53	0.30	0.19	−0.24
Exogone dispar	3.71	0.72	−0.68	0.47		−1.00
Filograna implexa	20.42		−1.00	63.87		−1.00
Luconacia incerta	3.27	0.36	−0.80	1.03	1.77	0.26
Malacoceros glutaeus	0.41		−1.00	0.81		−1.00
Podocerus sp. A	2.87		−1.00	0.27		−1.00
Syllis spongicola	2.15		−1.00	1.90		−1.00
Total	36.05	10.76		69.46	2.05	
Group B:						
Armandia maculata	0.22	10.75	0.96	0.03	0.19	0.73
Brachyura megalopae		6.09	1.00			0.00
Branchiostoma caribaeum			0.00	0.01	15.69	0.99
Calanopia americana		0.36	1.00		16.34	1.00
Caprella equilibra	1.55	2.87	0.30	0.34	1.40	0.61
Erichtonius brasiliensis	2.89	9.32	0.53	0.30	0.19	−0.24
Ervilia concentrica		0.36	1.00		48.18	1.00
Luconacia incerta	3.27	0.36	−0.80	1.03	1.77	0.26
Melita appendiculata	0.43	4.66	0.83	0.27		−1.00
Temora turbinata		4.30	1.00		0.28	1.00
Total	8.36	39.07		1.98	84.04	
Stomachs with food:		43			50	

predator on hard bottom areas (Sedberry and Van Dolah 1984), do not serve as "keystone" predators (Paine 1969) which influence community structure of invertebrates on South Atlantic Bight hard bottom reefs.

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GEORGE R. SEDBERRY

South Carolina Marine Resources Research Institute
P.O. Box 12559
Charleston, SC 29412

SEMILUNAR REPRODUCTIVE CYCLES IN *FUNDULUS HETEROCLITUS* (PISCES: CYPRINODONTIDAE) IN AN AREA WITHOUT LUNAR TIDAL CYCLES

Although lunar spawning rhythms are relatively common in species of shallow-water fish, semilunar reproductive cycles have been reported in a small but growing number of species (Korringa 1947; Johannes 1978). Species with the best documented semilunar gonad and spawning cycles include the California grunion, *Leuresthes tenuis*, (Clark 1925); Atlantic silversides, *Menidia menidia*, (Middaugh 1981); the tropical coral reef saddleback wrasse, *Thallassoma duperrey*, (Ross 1983); two tropical damselfishes, *Pomacentrus flavicauda* and *P. wardi*, (Doherty 1983), and gulf killifish, *Fundulus grandis*, (Greeley and MacGregor 1983); and the salt marsh mummichog, *Fundulus heteroclitus*, (Taylor et al. 1979; Taylor and DiMichele 1980). On the east coast of North America, *F. heteroclitus* move up onto marsh surfaces during high spring tides to spawn either in empty mussel (*Geukensia demissa*) shells or in the outer leaves of salt marsh plants (*Spartina alterniflora*) where oxygen levels are relatively high and sedimentation rates are relatively low (Able and Castagna 1975; Taylor et al. 1977; Kneib and Stiven 1978; Taylor and DiMichele 1983). Its eggs are extremely tolerant of desiccation and hatch on the next series of high spring tides. In addition, semilunar rhythms of larval hatching are well known for intertidal chironomid insects (Newmann 1978) and for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982).

In most cases, the proximal factors (sensu Giese and Pearse 1974) responsible for initiating and synchronizing these semilunar cycles are unknown. However, among the factors postulated as cues are tidal rhythms in water turbulence and hydrostatic pressures (Korringa 1947; Newmann 1978; Weld and Meier 1982; Ross 1983); tidal regimes in the habitat (Forward et al. 1982); photoperiod in combination with tidal fluctuations in water temperature (Miller et al. 1981), in combination with time of high tide (Middaugh 1981; Middaugh and Takita 1983), or in combination with interrupted current velocity (Middaugh and Hemmer 1984); and moonlight (Saigusa 1980). In addition to its wide distribution in coastal marshes with distinct lunar cycles of spring and neap tides, *F. heteroclitus* is abundant in extensive shoreline habitats and marshes of Chesapeake Bay, where tidal ranges are small and changes in water level caused by barometric pressure and wind frequently and unpredictably override lunar tidal levels and obliterate semilunar tidal cycles. In the present study, we measured the reproductive activity of *F. heteroclitus* in an area without lunar tidal cycles in order to determine if semilunar reproductive rhythms occur. The occurrence of semilunar reproductive rhythms would suggest that the proximal cues regulating the reproductive cycles are not factors associated with changes in tidal levels, such as pressure, or turbulence of currents.

Methods

This study was conducted from May through August 1982 at a small tidal creek (Muddy Creek) which flows into the Rhode River (lat. 38°51′N, long. 76°32′W), a subestuary on the western shore of central Chesapeake Bay, located about 11.3 km south of Annapolis, MD. The creek bottom consists of fine clays and silts, and its banks are fringed by a cattail (*Typha angustifolia*) marsh. Water level was measured with a Honeywell[1] diffused silicon differential pressure transmitter (accurate to ± 1.238 cm) at a station operated by the U.S. Geological Survey on the Rhode River near the mouth of Muddy Creek about 1,000 m from the site where fish were sampled. Changes in water level at the monitoring station accurately reflect water levels at the sampling site (D. L. Correll[2] and R. L. Cory[3]). Measured daily high water levels were compared with predicted high tidal levels published for the Rhode River (National Oceanic and Atmospheric Administration 1981).

Fundulus heteroclitus is the most abundant fish in the creek (Hines unpubl. data). Fish were sampled every 2-3 d during the hours of 0730-1230, using unbaited minnow traps set just above low water level. Each sample consisted of 8-12 males and 8-12 females which were tested for readiness to spawn, and another 8-12 of each sex were taken to determine gonad indices. Readiness to spawn was determined in the field by applying gentle pressure from anterior to posterior along the ventral surface of the fish. Release of sperm or eggs was interpreted as the fish being ripe. The gonad index for each fish in the sample was determined by dissecting out the testes or ovaries and by drying the gonad and body to constant weight at 60°C and weighing them to the near-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]D. L. Correll, Assistant Director, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, pers. commun. September 1982.

[3]R. L. Cory, Oceanographer, U.S. Geological Survey, Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037, pers. commun. September 1982.

est 1×10^{-5} g. The gonad index equals the (gonad weight/body weight) $\times$ 100.

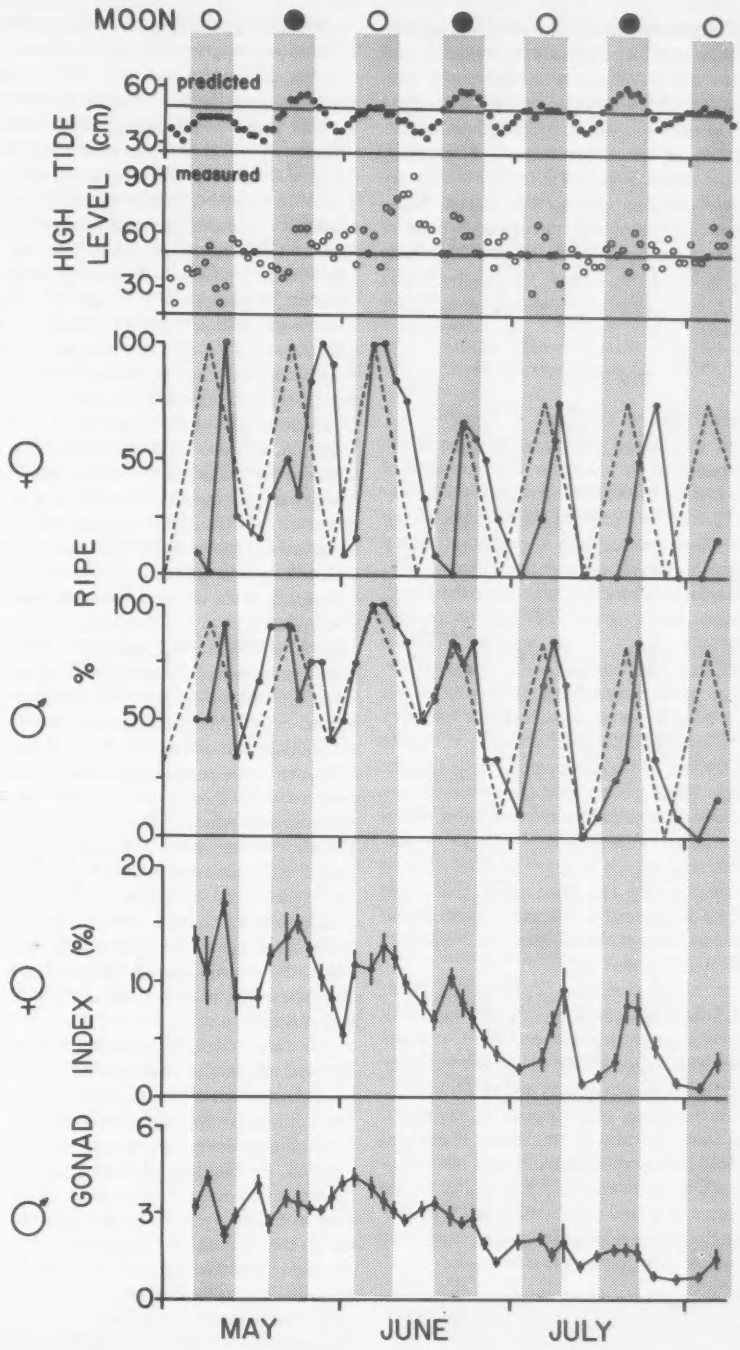
Results

Although tides in the Rhode River subestuary exhibited an approximately semidiurnal rhythm, fluctuations in measured high tide level were not correlated with predicted high tide level (product moment correlation of log transformed data for daily predicted and measured high tide, $r = 0.111$; Student's t-test for $r \neq 0$, $P > 0.2$; Fig. 1). Moreover, time series spectral analysis (Thrall and Engelman 1981) showed that measured tides exhibited only a very weak peak in spectral density at a frequency of about 12.5 d rather than the strong peak of 7.5 d exhibited by predicted tidal cycles. Cross correlation between predicted and measured tides in bivariate spectral analysis showed low and variable coherence ($P > 0.05$). Similarly, linear association of the two variables was weak, with variable phase shifts and variable coefficients necessary to fit one variable to the other. In addition, the occurrence of tides sufficiently high to flood the marsh fringing the creek (i.e., tides > 46 cm) did not occur more frequently at night than during day (χ^2 test, $P > 0.2$), nor more frequently during any particular lunar phase (χ^2 test, $P > 0.4$). High tides did not occur consistently during any 2-h period of the 24-h day at the quarters of the new or full moons (χ^2 test, $P > 0.4$). Thus, water levels in the estuary were neither predictable in amplitude within the tidal range nor related in any obvious cyclical pattern to the lunar cycle.

However, both female and male *F. heteroclitus* showed distinct semimonthly cycles in readiness to spawn from May through August (Fig. 1). Females and males also exhibited a distinct semimonthly cycle of gonad size, although the cycle of male gonad index was not as pronounced as that of females, due to the small changes in size of the testes during spawning (Fig. 1). The cycles of spawning readiness in males and females were usually in phase with the lunar cycle. Comparisons of the observed frequencies of spawning readiness with frequencies predicted by cycles with perfect semilunar periods and the same amplitudes showed no significant differences in 27 of 37 d of observation for females and 33 of 37 d of observation for males (χ^2 test, $P < 0.05$). Observed frequencies of spawning readiness over the entire study period were not significantly different from frequencies predicted by the perfect semilunar cycles for either females or males (χ^2 test, $P > 0.2$). Although six out of six peaks of spawning readiness for males occurred during the 7 d surrounding new or full moons, for females only four of the six peaks occurred during the first or last quarters of the moon, indicating that for the small numbers of peaks occurring during a reproductive season, readiness to spawn does not coincide with new and full moons (Fisher's Exact Test for number of spawning peaks occurring within the specified period, $P = 0.227$; Fig. 1). However, if the timing of the peaks in readiness to spawn is considered to lag 3.5 d after the new and full moons, then all peaks for males and females occurred within the 7 d surrounding the lagged period, indicating a significant synchronous semilunar cycle (Fisher's Exact Test on number of peaks occurring within the specified period, $P < 0.01$). Female spawning was correlated with male spawning (product moment correlation of arcsine transformed spawning frequencies, $r = 0.695$; Student's t-test for $r \neq 0$, $P < 0.001$). However, neither female nor male readiness to spawn was correlated with the measured tides (product moment correlation of arcsine transformed frequencies of spawning readiness with log transformed high tide measurements, $r = 0.184$ for females and $r = 0.272$ for males; Student's t-tests for $r \neq 0$, $P > 0.2$). Thus the semilunar cycles of spawning readiness of both sexes appeared to be synchronized, but not to be related to the tidal regime of the estuary.

The reproductive season of *F. heteroclitus* in the Rhode River-Muddy Creek estuarine system occurred from late April to September, when water temperatures were above 17°C (pers. obs.). Mean gonad indices of female and male samples declined during the season, both at the peak and at the spent phases of the semimonthly cycles (Female Gonad Index = -0.124 Day + 14.1 and Male Gonad Index = -0.035 Day + 3.83; Student's t-test for slopes $\neq 0$, $P \leq 0.05$; (Fig. 1)). The decline of mean gonad index during the season reflected two statistics. First, an increasing percentage of the population failed to initiate gonad recrudescence during successive cycles.

FIGURE 1.—Lunar phase, tidal levels, and reproductive cycles of *Fundulus heteroclitus* from May to August 1982 in a tidal creek on central Chesapeake Bay. Full moons (open circles) and new moons (solid circles) are indicated. Daily high water levels above mean low water are shown for measurements at the study site and for tidal levels predicted by National Oceanographic and Atmospheric Administration (1981). Horizontal lines indicate water level which floods the marsh adjacent to the Creek. The percentages of female and male fish which were ready to spawn are shown for each sample throughout the spawning season (solid lines), along with hypothetical spawning cycles with the same amplitudes and perfect semilunar periods in phase with the new and full moons (dashed lines). Gonad indices (mean ± SE) for females and males are also plotted for each sample.


MOON
HIGH TIDE LEVEL (cm)
predicted
measured
60
30
90
60
30
♀
% RIPE
100
50
0
♂
100
50
0
♀
GONAD INDEX (%)
20
10
0
♂
6
3
0
MAY
JUNE
JULY

None of the female fish sampled on the May spawning peaks had undeveloped gonads (individual gonad indices were all > 10%), whereas many had undeveloped gonads on the July peaks (38% of the sample for gonad weights had individual indices < 5%, and 25% of the sample tested for spawning were not ripe). Second, gonad size of fish with developed gonads declined during the season. Mean gonad indices of females with developed ovaries of the May peaks were significantly greater than those of the July peaks (15% versus 9%, respectively) (Student-Newman-Keuls test of arcsine transformed data, $P < 0.05$).

Discussion

In *Fundulus heteroclitus* and *F. confluentus*, regulation of the annual reproductive cycle is apparently dependent on changing combinations of photoperiod and temperature (Harrington 1959; Day and Taylor 1982). The decline in gonad index during the season in the present study is consistent with a similar decline observed by Kneib and Stiven (1978) and Taylor et al. (1979) and suggests that, along with physical factors, energy availability may be limiting reproductive output late in the season. Weisberg (1981) found that supplemental food increased the gonad indices of *F. heteroclitus* in Delaware salt marshes. Histological evidence shows that primary oocytes in *F. heteroclitus* can undergo complete development in one biweekly spawning cycle (Taylor and DiMichele 1980), so lag time for recrudescence of spent gonads does not account for reduced reproductive activity late in the season. *Fundulus grandis* reproduces throughout the summer in some areas of the gulf coast (Greeley and MacGregor 1983), but shows bimodal reproductive activity in spring and fall with no reproduction in midsummer in shallow ponds (Waas and Strawn 1983).

In addition to *F. heteroclitus* (Taylor et al. 1979; Taylor and DiMichele 1980), semilunar spawning cycles occur in some populations of *F. grandis* (Greeley and MacGregor 1983), *F. similis* (Greeley 1982), *F. majalis* (Tedesco et al.[4]), and probably in *F. notatus* (inferred from observations of spawning behavior in Carranza and Winn 1954). Waas and Strawn (1983) measured a weak lunar, but not a semilunar cycle in populations of *F. grandis* in two nontidal ponds and a tidal creek with lunar tides frequently overridden by wind effects. The semilunar spawning cycle in *F. grandis* has been induced in the laboratory during their reproductive season by interaction of photoperiod and tidal changes in water temperature shifting on a lunar cycle (Miller et al. 1981). Daily disturbances (netting) of *F. grandis* also apparently induces circadian gonadal responses (Weld and Meier 1982). Tidal rhythms in water turbulence and hydrostatic pressure have been postulated for lunar and semilunar reproductive rhythms in fish (Korringa 1947; Ross 1983) and for semilunar hatching in intertidal chironomid insects (Newmann 1978). Middaugh (1981) suggested that the biweekly coincidence of a high tide at the time of sunrise and/or a lunar cue may serve as a synchronizer for spawning of *Menidia menidia* in a South Carolina estuary. In contrast to *M. menidia*, which showed a precise reproductive response to diurnal tidal and lighting schedules (Middaugh and Takita 1983), *M. peninsulae* exhibited a variable and labile response in which a combination of semidiurnal interruptions of current and diel light cues was optimal at inducing spawning synchrony (Middaugh and Hemmer 1984). However, this synchrony in *Menidia* spp. had a diel period, and the laboratory experiments were not run long enough to test for lunar rhythms. Semilunar rhythms of larval hatching are well documented for several species of intertidal and estuarine crabs (see Christy 1982; Forward et al. 1982). Hatching in the mud crab, *Rhithropanopeus harrisii*, followed a semilunar and diurnal rhythm in populations from an estuary with semidiurnal and lunar tidal cycles, whereas hatching was not associated with lunar rhythms or tidal levels in an estuary with aperiodic tides (Forward et al. 1982). Moveover, Forward et al. (1982) induced circatidal rhythms in larval release in crabs from an estuary with irregular tides by transplanting them to an estuary with semidiurnal and lunar tides. However, Saigusa (1980) showed that the larval hatching cycle of a semiterrestrial crab *Sesarma haematocheir* is entrained directly by a moonlight cycle.

In the present study, in an area without a lunar periodicity in the tidal cycle, *F. heteroclitus* had a semilunar reproductive cycle which lagged the new and full moons by 3.5 d. Although the study area had tidal fluctuations with an approximately semidiurnal period, the diel timing of high tides with respect to photoperiod also did not appear to cue the semilunar reproductive cycle. Changes in currents associated with the diurnal tidal cycle may serve as a synchronizing cue for the time of day of spawning, as it does for *Menidia menidia* and *M. peninsulae*. However, while identity of the cue remains unknown, the present study indicates that tidally mediated factors such

[4]Tedesco, M., A. H. Hines, and L. A. Wiechert. 1983. Semilunar gonadal cycles in *Fundulus majalis* (Pisces: Cyprinodontidae). Technical Report of Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, MD 21037.

as turbulence, hydrostatic pressure, temperature, and salinity are not responsible for synchronizing the semilunar rhythm.

Hypotheses concerning the ecological consequences and adaptive significance of semilunar cycles of larval release in *Uca* spp. and other estuarine crabs have been discussed recently by Christy (1982). His analysis indicates that convergence among estuarine crab species in the semilunar timing of larval release results in rapid seaward transport of larvae, which minimizes the effects of lethal combinations of high temperature and low salinities or intense predation in the upper estuary. However, *Rhithropanopeus harrisii* completes its larval development within the upper reaches of estuaries and shows a variable cycle of hatching, depending on tidal predictability, which may be advantageous for retention of larvae within the estuary (Forward et al. 1982). Lunar spawning cycles of insular coral reef fish may have evolved to solve similar problems of larval dispersal away from predators while assuring return of the recruits to the adult habitat (Johannes 1978; Ross 1983). Semilunar spawning cycles of *Fundulus heteroclitus*, *Menidia menidia*, *Leuresthes tenuis*, and other fish which spawn in the upper intertidal zone (Taylor and DiMichele 1983; Middaugh 1981; Clark 1925) may have the adaptive advantage of removing spawning adults and eggs from subtidal predators. Although the eggs of *F. heteroclitus* are tolerant of desiccation (Able and Castagna 1975; Taylor et al. 1977), the major advantage of the spawning site appears to be higher oxygen levels and reduced sedimentation than in the creek (Taylor and DiMichele 1983). However, spawned eggs of *F. heteroclitus* and *M. menidia* are usually found in areas inundated daily by high tides (Middaugh 1981). In the present study, 62% of the days had tides which flooded the marsh (Fig. 1), where eggs are probably deposited in the bases of leaves of *Typha angustifolia* plants (see Taylor and DiMichele 1983). Although there may be additional advantages in areas with predictable tidal fluctuations with lunar periodicity, the major advantage of semilunar spawning rhythms in *F. heteroclitus* appears to be improved fertilization success afforded by synchronized spawning.

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ANSON H. HINES
KENRIC E. OSGOOD
JOSEPH J. MIKLAS

Smithsonian Environmental Research Center
P.O. Box 28
Edgewater, MD 21037

UNDERSEA TOPOGRAPHY AND THE COMPARATIVE DISTRIBUTIONS OF TWO PELAGIC CETACEANS

Prey species are not uniformly distributed. Foraging efficiency, therefore, should be maximized when effort is concentrated in areas where prey are concentrated. Cetacean food is probably most concentrated in regions of high general productivity. Because the undersea topography may be a major influence on productivity, cetacean foraging patterns may be associated with the topographic patterns of the ocean floor (Hui 1979). I report here the occurrences of two species of pelagic odontocete cetaceans, the Pacific pilot whale, *Globicephala macrorhynchus*, and the common dolphin, *Delphinus delphis*, relative to seafloor topography and to diet. Although it is not clear if the genus *Delphinus* in this region is composed of two species or one species with two subspecies, the vast majority are *Delphinus delphis* (Banks and Brownell 1969; Evans 1975). If data from more than one species are included in this study, it is assumed that any interspecies difference in distribution relative to substrate was not significant to the analyses.

Methods and Results

This study was conducted in the Southern California Continental Borderland (Fig. 1) which consists of ridges, deep troughs, and basins (Chase 1968). There were 61 survey flights totaling 22,353 km. The flights were conducted at various times, all of them during midday (1000-1500) from 1968 through 1976. Totals of 1,057 pilot whales in 38 aggregations (in January, March, April, July, October, and December) and 47,105 common dolphins in 142 aggregations (in all months of the year) were observed. The survey methods have been previously described (Hui 1979).

The data for each species were not divided into temporal subsets as in Hui (1979), but were treated as whole sets. The distribution of each species was examined relative to depth and relative to change in depth. The method of analysis has been presented in detail elsewhere (Hui 1979).

Both pilot whales and common dolphins were distributed uniformly ($P > 0.10$) throughout the depth classes but not uniformly among the Contour Index (CI) classes ($P < 0.005$). For each species there were more observations than expected over the steepest bottom topography and fewer than expected over the flattest (Table 1).

I also compared the distribution of pilot whales

among CI classes to the distribution of common dolphins. Due to the small number of pilot whale aggregations, the CI range was divided into four unequal classes to meet the statistical assumptions for chi-square analysis (Dixon and Massey 1969). The proportion of pilot whales in each of these classes

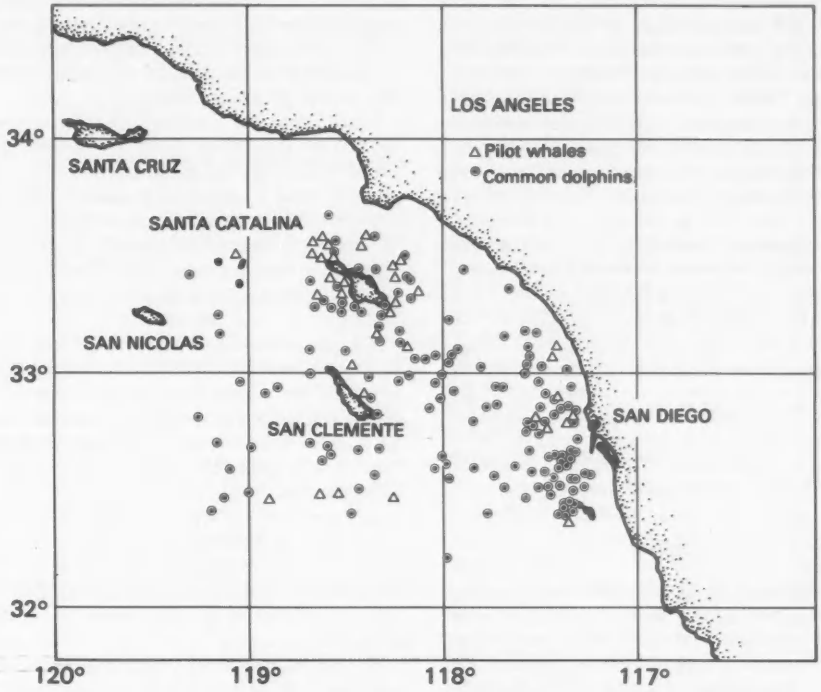

FIGURE 1.—Sightings of pilot whales, *Globicephala macrorhynchus*, and common dolphins, *Delphinus delphis*. The study area is bounded on the west by long. 120°00'W and on the east by the coast of California between lat. 34°05'N and 32°24'N. Sightings may not accurately depict the geographic distribution of these species because the survey flights were not uniformly distributed spatially or temporally. Encounters occurring outside the study area are not shown.

TABLE 1.—Distribution among contour index classes of observed and expected aggregations (see text).

Species	Contour index class	Number of aggregations		$(F-f)^2$
		Expected (F)	Observed (f)	F
Pilot whales	0.01-19.99	13.3	1	11.38
	20.00-39.99	6.3	5	0.27
	40.00-59.99	5.2	4	0.28
	60.00-79.99	7.4	10	0.91
	80.00-99.99	5.8	18	25.66
				χ^2 = 38.50
Common dolphins	0.01-19.99	48.0	18	18.75
	20.00-39.99	23.2	27	0.62
	40.00-59.99	19.3	22	0.27
	60.00-79.99	27.2	21	1.41
	80.00-99.99	22.2	54	45.55
				χ^2 = 66.60
				χ^2 (df = 4, P = 0.005) = 14.86

was used to compute the expected number of common dolphins in that class.

The distribution of pilot whales was not the same as that of common dolphins among the CI classes ($P < 0.005$), particularly in the class for the lowest relief. Of the total chi-square value, 63% is due to proportionally more observations of dolphins than pilot whales in this one class (Table 2).

The distributions of the two sets of survey flights used to collect data for the two species were compared, but the CI range in this case was divided into 10 equal classes. The two sets of survey flights were equally distributed among the CI classes ($P > 0.10$).

TABLE 2.—Comparative distribution among contour index classes of pilot whales and common dolphins.

Contour index class	Dolphin aggregations		$(F-f)^2$
	Expected (F)[1]	Observed (f)	F
0.01-39.99	22.4	45	22.80
40.00-59.99	14.9	22	3.38
60.00-79.99	37.4	21	7.19
80.00-99.99	67.3	54	2.63
		χ^2 =	36.00
		χ^2 (df = 3, P = 0.005) =	12.84

[1]Computed from pilot whale sightings, see text.

Discussion

In the California Bight, pilot whales and common dolphins are distributed similarly above undersea topography of high relief, but common dolphins occur more frequently than pilot whales over areas of low relief. This difference may be linked to differences in feeding habits.

Pilot whales and common dolphins have significant morphological and physiological differences that are associated with their foods and feeding methods. Pilot whales are larger (7 m vs. 2 m in length) and have fewer but larger teeth (40 vs. 200) than common dolphins (Orr 1972). Pilot whales are capable of diving to 610 m (Bowers and Henderson 1972) while common dolphins dive to 257 m (Evans 1971).

The diet of the common dolphin in the Southern California Bight includes 19 species of fish, 2 species of squid, and miscellaneous crustaceans (Fitch and Brownell 1968; Evans 1975).

In contrast to common dolphins, pilot whales appear to be stenophagous, eating primarily squid. Atlantic pilot whales, *Globicephala melaena*, eat primarily squid (*Illex illecebrosus*). The only fish reported eaten (cod, *Gadus morhua*) composes <10% of the diet (Sergeant 1962). There has been no study on the Pacific pilot whale comparable with that of Sergeant's (1962) on the Atlantic form; however, the stomachs of four wild Pacific pilot whales have been examined. They contained squid but no fish (W. A. Walker,[1] C. W. Woodhouse,[2] D. J. Seagars[3]). In captivity an Atlantic pilot whale rejected mullet (Mugilidae) and blue runner (Carangidae) fish and accepted only squid (probably *Loligo pealei*) until it was tricked into eating some herring (Clupeidae); and then the indications were that "He did not seem to digest the fish as well" (Kritzler 1949).

Squid distribution cannot be related to any particular bottom topography along the California coast because squids are not easily collected with sampling methods used in distribution studies (Mais 1974). However, it may be inferred that the narrow range of seafloor topographies visited by pilot whales reflects the narrow range of their diet and the areas where squid can be most easily caught by pilot whales.

Also concentrated over areas of canyons and escarpments are anchovies (Mais 1974), a major component of the dolphin diet (Fitch and Brownell 1968; Evans 1975). Common dolphins frequent these areas most. However, common dolphins are euryphagous. Some prey probably occur over seafloor of low relief, although this could not be confirmed from fish reports because bottom topography is not a parameter which is recorded in fish distribution studies. If some prey do occur over areas of low relief, their distribution would partially explain why dolphins occur over seafloor of low relief more frequently than do pilot whales.

My analyses show that the daytime distribution patterns of these two pelagic cetacean species are not random but are related to bottom topography. Although the distributions are similar, they are not the same. Differences in distributions may be due to the different foraging patterns but no firm conclusion can be drawn until more information is available.

Acknowledgments

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[1]W. A. Walker, Research Associate, Section of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, CA 90007, pers. commun. July 1980.

[2]C. W. Woodhouse, Curator of Vertebrate Department, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105, pers. commun. July 1980.

[3]D. J. Seagars, Wildlife Biologist, National Marine Fisheries Service, Southwest Region, 300 S. Ferry St., Terminal Island, CA 90731, pers. commun. January 1981.

stomach contents of Pacific pilot whales. My special thanks to W. E. Evans of Hubbs Sea World Research Institute for his support and encouragement throughout this study, which was supported by ONR contract T0044 subproject RR0310201 (W. E. Evans, principal investigator), and NMFS agreement 01-6-200 11439.

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CLIFFORD A. HUI

Chemistry and Biochemistry Branch, Code 521
Naval Ocean Systems Center
San Diego, CA 92152-5000

LARVAL AND JUVENILE GROWTH OF SABLEFISH, *ANOPLOPOMA FIMBRIA*, AS DETERMINED FROM OTOLITH INCREMENTS

The black cod or sablefish, *Anoplopoma fimbria*, has been the subject of an intensifying fishery off the west coast of North America over the last decade. Biological information on this species, however, including data on spawning, early life history, age and growth, and population structure, is relatively meager. Sablefish are widely distributed in the northern Pacific, with adults most abundant at depths of 366-915 m (Hart 1973). Mason et al. (1983) suggested that eggs are spawned and developed in waters deeper than 300 m and colder than 6°C off Canada. Juveniles occur in shallow water, however, and larvae are almost exclusively neustonic (Kendall and Clark[1]). Thus larval development and growth occur in much warmer water than that inhabited by later stages, particularly in the southern portion of the species range.

Sablefish growth has been described by Heyamoto (1962) and Pruter (1954), among others, who used scale annuli to define the growth pattern. More recent work, however, has shown that the age estimates, particularly for older, mature fish, are in error; growth is apparently much slower and longevity much greater than previously thought (Beamish and Chilton 1982). The warmer neustonic habitat of the larvae may result in different growth patterns in early life; ontogenetic changes in growth and habitat are relatively common among deeper living fishes (Boehlert 1982; Luczkovich and Olla 1983). The only observations on growth of young sablefish are those of Heyamoto (1962), who suggested that juveniles of 12-16 cm fork length (FL) were about 6 mo old. In the present study we report on the growth of field-collected larval and juvenile sablefish where age was estimated by enumerating growth increments on the otoliths.

Materials and Methods

Larval and juvenile sablefish were collected in 1981-83. Larvae were taken in 0.5 m neuston nets (Sameoto and Jaroszynski 1969) with 0.505 mm mesh, off the coasts of Oregon and Washington during May 1982 by the RV *Poseydon*. Samples were immediately preserved in 80% ethanol. After sorting,

[1]Kendall, A. W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and northern California, April-May 1980. Processed Rep. 82-11, 44 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98102.

larvae were stored in individual vials labeled with sample number and date. Additional larvae were collected with neuston nets in May 1983 by the RV *Ekvator*. Larger juveniles (> 70 mm standard length (SL)) were taken in a small mesh purse seine deployed from 24 to 40 km off of the Oregon-Washington coasts during the summer months of 1981 (Fig. 1). Specimens were frozen on board and held until measurements and otoliths were taken. Fork lengths to the nearest millimeter were recorded for these larger juveniles and standard lengths to the nearest 0.1 mm were measured for all larvae and small juveniles. No corrections were made for potential shrinkage from preservation of young larvae, but alcohol preservation causes no noticeable shrinkage in length of anchovy larvae (Theilacker 1980). For subsequent analysis, fork lengths were converted to standard length by the relationship SL (mm) = 0.91 FL (mm) − 1.15 (n = 54, r^2 = 0.999), which was based upon specimens 21.7 to 297 mm FL.

Otoliths of larval sablefish were removed and cleaned under a dissecting microscope fitted with polarizing filters. Increments on otoliths from larvae < 26 mm SL were clearly visible from the focus to the margin (Fig. 2); these otoliths were left intact, affixed to microscope slides with histological mounting medium and cover slips, and increments were read in the sagittal plane (see Taubert and Coble 1977 for terminology). For larger larvae and most juveniles, a sagittal section of the otolith provided the clearest increments. The left otolith of every pair was mounted in histological medium on a microscope slide and the

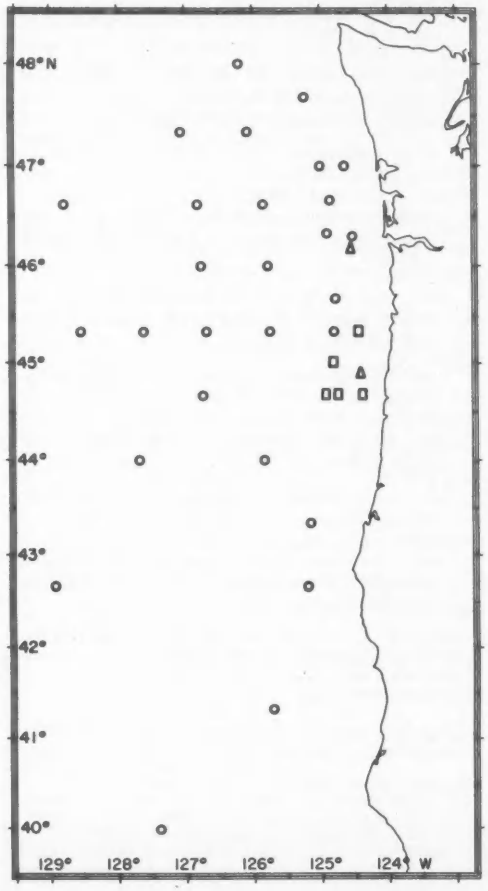

FIGURE 1.–Distribution of *Anoplopoma fimbria* samples, along the Pacific coast, used for age and growth analysis. Circles represent the neuston samples taken during May 1982, triangles represent the purse seine samples taken during summer 1981, and squares represent the 1983 neuston samples.

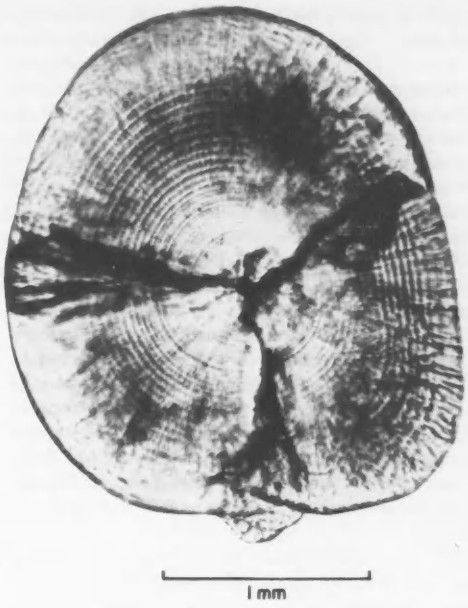

FIGURE 2.—Sagitta otolith from a larval *Anoplopoma fimbria* (22.0 mm SL; duplicate increment counts were 37 and 40 d). Scale bar = 0.1 mm.

internal surface was ground until the focus was visible. The microscope slide was heated and the section was turned over to expose the external surface. Grinding and polishing continued, while care was taken to insure that material was not lost from the margin. The result was a clear, thin section of the otolith in the sagittal plane. For some of the larger juveniles (> 100 mm SL), transverse sections were cut from the otoliths using a diamond saw, mounted on microscope slides, and ground to make the increments clear. All otoliths were read under a compound microscope at 400× or 1,000× magnification. Two independent counts were made for each otolith. These counts were made at least 2 wk apart; the age assigned to each specimen was the mean of the two counts.

Increments, comprised of adjacent light and dark ring pairs, were distinct and clear in the smallest otoliths (Fig. 2), but interpretation became more difficult as the increments became progressively smaller and as changes in growth patterns occurred in the otolith structure of the older specimens. There was no evidence of subdaily patterns in the increments, and each increment was assumed to represent 1 d. Support for the daily deposition of increments was provided by data on three live juvenile sablefish held in the laboratory (Table 1). The specimens were captured by neuston net off Newport, OR, and transported to the laboratory where they were fed to satiation daily on *Artemia*. A check, apparently associated with capture and transfer to the laboratory, was evident on the otolith of each fish. The numbers of increments past this check corresponded closely to days captive; the minor differences are attributed to counting error and/or difficulty in interpretation of the check (Table 1). We thus consider the increments to be deposited with a daily periodicity. Hereafter increment counts will be equated with days after first increment formation; as we discuss later, first increment formation may occur at first feeding.

Data from the 1982-83 larval collections and the 1981 juvenile collections were fitted separately with simple linear regressions. Nonlinear curves (exponential, logistic, and Laird-Gompertz) were fitted to combined data with the NLIN procedure on the SAS[2] statistical package (SAS Institute, Inc. 1982).

TABLE 1.—Growth and increment formation in captive specimens of *Anoplopoma fimbria*. L_1, L_2; standard length (mm) at capture and death, respectively.

Capture date	L_1	L_2	Days captive	Increment past check	Total increments
2 May 1983	19.9	60.4	31	31	63
17 May 1983	14.1	53.4	40	38	95
24 May 1983	53.8	109.7	32	33	87

Results and Discussion

This study considers a total of 105 individuals, including 71 larvae and juveniles (9.8 to 41.2 mm SL) from the 1982 neuston collections, 21 juveniles (102.8 to 259.6 mm SL) from the 1981 purse seine collections, and 13 larvae (10.4 to 25.3 mm SL) taken in the 1983 neuston collections. Mean increment counts ranged from 9 increments for the youngest larva to 180 increments for the oldest juvenile. The abundance of larval sablefish in the neuston (Kendall and Clark footnote 1) at such young ages suggests that larvae move rapidly after hatching from the deep spawning region rather than early growth occurring at depths as suggested by Mason et al. (1983). The difference between the two increment counts for each otolith increased with increasing count, but the coefficient of variation remained the

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

same for the two ranges. For the larvae collected in 1982, with an overall mean of 30.8 increments, the mean difference was 1.67 increments (n = 71, standard deviation (SD) = 1.45). For the 1981 juvenile collections, with overall mean of 109.5 increments, the mean difference between the two estimates was 6.57 increments (n = 21, SD = 5.03).

Growth rates of field-collected larval and juvenile sablefish differ considerably. The data for the 1982 larval collections is described by the line

$$\text{SL} = 0.375\ (\text{age, d}) + 5.27$$
$$n = 71,\ r^2 = 0.838,$$

suggesting a mean growth rate for small larvae of 0.375 mm/d and an intercept of 5.27 mm, which coincides with the size of newly hatched larvae (Mason et al. 1983). Similarly the 1981 juvenile data is described by the line

$$\text{SL} = 1.469\ (\text{age, d}) - 0.926$$
$$n = 21,\ r^2 = 0.822,$$

suggesting a mean growth rate of 1.47 mm/d. Certain of these growth differences may have been a function of gear selection. If net avoidance is a function of fish size, as for most other planktonic organisms (Barkley 1972), then the oldest specimens taken in the neuston gear may have been only the slow-growing members of that cohort. Alternatively, interruptions of increment formation, resulting in underestimates of age, may occur. This has been observed for some species by Geffen (1982). In the laboratory specimens, however, one individual (L_2 = 60.4 mm SL, Table 1) ceased eating for 5-6 d, became emaciated, and died. The last five increments near the margin were smaller than the remainder, but the 1:1 correspondence of days to increments suggests that increment formation continued.

Estimated age-at-length data from all years were combined to describe the growth of sablefish to an age of about 200 d. Comparing exponential, logistic, and Laird-Gompertz growth models, the best fit (as judged by residual sums of squares) was provided by the Laird-Gompertz growth model (Fig. 3) in the form:

$$L_t = L_0\ (A_0/\alpha)\ (1 - \exp\ (-\ \alpha t))$$

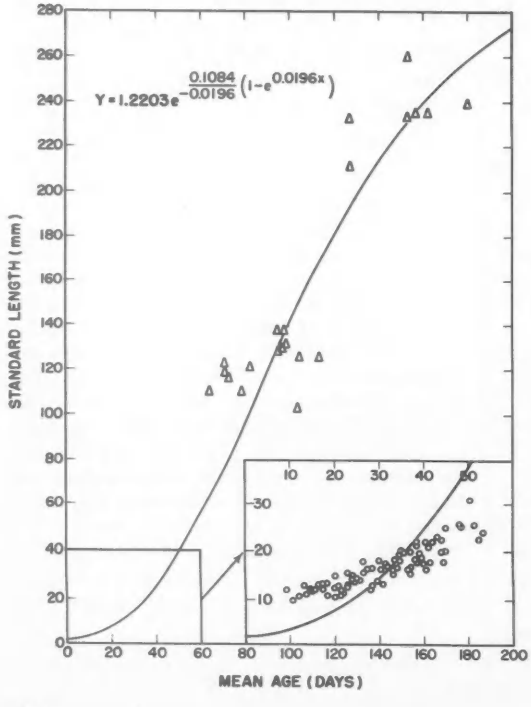

FIGURE 3.—Estimated age at length for all *Anoplopoma fimbria* in the study. Specimens taken in neuston nets (n = 84, including the 13 from 1983) are represented by circles, 1981 juvenile specimens from purse seine collections (n = 21) are represented by triangles. The equation and line represent the least squares fit of the Laird-Gompertz growth model.

where L_t = standard length (mm) at age t (d), L_0 = initial length (y-intercept), and A_0 and α are fitted parameters (Table 2).

This sigmoid curve suggests relatively slow growth to an age of about 50 d and a length of about 25 mm SL, followed by rapidly accelerating growth through the juvenile stage, an inflection point at 113.2 mm, and an asymptotic length near 307.8 mm. Since sablefish achieve lengths to 100 cm (Hart 1973), these results should not be extrapolated beyond the ages in the present study. Also, the predicted fit of zero age individuals (L_0) is 1.22 mm SL (Table 2; Fig. 3). This value does not accurately reflect the length of sablefish at hatching. Egg size in sablefish ranges from 1.8 to 2.2 mm and newly hatched larvae are 5 to 6 mm (Mason et al. 1983). If daily increments are first laid down at first feeding as in some other species (Laroche et al. 1982), then this intercept is clearly an underestimate. Mean egg size suggests a length at first feeding of about 8 mm (Shirota 1970). The smallest larva taken in the present study was 9.8 mm SL (Fig. 3). This part of the curve may be related to the inclusion of the older, slower growing neustonic specimens. Another factor may be effects of shrinkage; small specimens were preserved in ethanol, older juveniles frozen. The magnitude of shrinkage for *A. fimbria* is unknown, but capture and preservation of other fish larvae causes shrinkage which decreases with increasing age or size (Theilacker 1980). Thus increases in actual length for small individuals may have been relatively greater, changing the fitted equation and possibly increasing the length at time zero (Fig. 3).

Heyamoto (1962) estimated growth for young sablefish, suggesting that specimens 12.3 to 16.4 cm FL (11.1 to 14.8 cm SL) were 6 mo old. His data, however, were based upon estimating the age at collection by difference between capture and an assumed spawning season. In our study, 6-mo-old specimens were > 24 cm SL. The specimens captured by Heyamoto (1962) were taken by trawl in 320 to 412 m, much deeper than the epipelagic juveniles in our study. Beamish et al. (1983) used daily increments as part of a study to validate annulus formation in sablefish. In nine specimens 23 to 27 cm FL (208 to 245 mm SL), they observed from 270 to 350 (mean 313) increments but suggested that the fish were 1 yr old due to the inability to count all increments. Based upon our growth curve (Fig. 3), their ages would be overestimates.

Recent observations of laboratory growth are in substantial agreement with growth described by our curve. Shenker and Olla[3] found average growth rates as high as 2.3 mm/d for juvenile sablefish fed ad libitum. These fish were near the lengths where our curve predicts fastest growth (2 mm/d, Fig. 3). High growth rates were also observed for fish smaller than 25 mm, where our data suggest relatively slow growth. Grover and Olla[4] noted starvation of field-collected sablefish larvae based upon morphological criteria; thus food probably limits sablefish growth in the field. This species apparently has a great scope for growth given high laboratory rations or patches of high prey density in the field.

TABLE 2.—Fitted parameters of the Laird-Gompertz growth model for larval and juvenile *Anoplopoma fimbria* in the present study. The curve is fitted to all larvae and juveniles (N = 105) based upon counts of otolith increments.

Parameter	Estimate	Asymptotic standard error
L_0	1.2203	0.4675
A_0	0.1084	0.0146
α	0.0196	0.0015

The distribution of dates of first increment formation were estimated by back calculating from the ages of all specimens in our study. Since larvae and juveniles were from different years and sampling gears, it is possible that differences would be observed in this distribution. Since the plankton gear selects for smaller larvae due to avoidance by later stages, the results could be biased if the entire spawning season were not sampled. The median dates for the 1982 larvae (8 April) and the 1981 juveniles (18 March), however, were similar. Thus all 105 samples were combined and the distribution of the dates of first increment formation plotted (Fig. 4). The distribution has a mode in early April. If the first increment is formed in association with first feeding, as in most other species studied (Brothers et al. 1976; Taubert and Coble 1977; Laroche et al. 1982), then the spawning dates would precede the distribution in Figure 4. Ware (1975) provided an egg size-incubation time relationship for fishes; sablefish, with a 2 mm egg, would have an incubation time of 13 d. If a similar time is spent in yolk absorption before first feeding, peak spawning would occur in early March. This generally agrees with most other reports of the spawning season for *A. fimbria*.

[3]Shenker, J., and B. L. Olla. Laboratory growth and feeding of juvenile sablefish, *Anoplopoma fimbria*. Unpubl. manuscr.

[4]Grover, J., and B. L. Olla. Field evidence for starvation of larval sablefish, *Anoplopoma fimbria*. Manuscr. in prep. Northwest and Alaska Fisheries Center, Newport Field Office, National Marine Fisheries Service, NOAA, c/o Marine Science Center, Marine Science Drive, Newport, OR 97365 (direct correspondence to B. L. Olla).

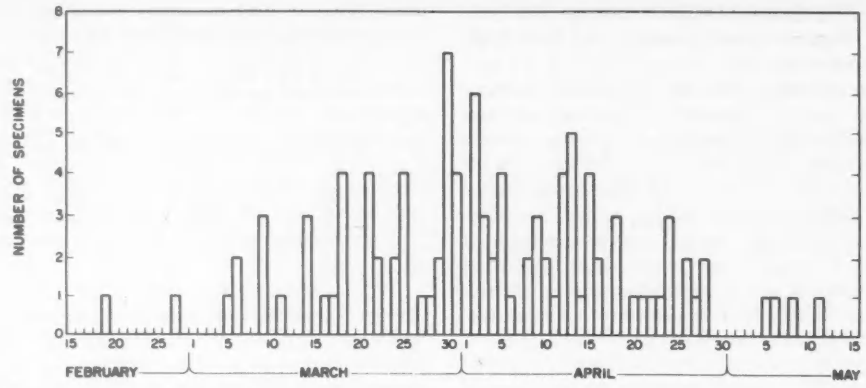

FIGURE 4.—Distribution of dates of first increment formation for *Anoplopoma fimbria*, determined by back-calculations using age and collection date.

Phillips (1958) defined the peak spawning season off California to be January-February. Bell and Gharrett (1945) suggested that the spawning season was around December off Washington based upon fishermen's observations and the presence of spent females in January. Farther north, Thompson (1941) observed ripe females and fertilized eggs in March at Cape St. James (lat. 51°45'N). More recent work has shown that the spawning season off British Columbia occurs in January to February with the peak of spawning in February (Mason et al. 1983).

Our observed growth rates for *A. fimbria* during the first 6 months of life are high for a temperate-subarctic species, yet are clearly below the potential growth rate as shown in the laboratory (Shenker and Olla footnote 3). Similar but lower laboratory growth rates (1.2 mm/d) were observed for 100 to 150 mm juvenile red hake, *Urophycis chuss*, by Luczkovich and Olla (1983). Both of these species contrast markedly with larval juvenile growth in other taxa. Boehlert and Yoklavich (1983), for example, summarized laboratory and field growth measurements for 13 species in the genus *Sebastes* and noted growth rates ranging from 0.092 to 0.590 mm/d. Young sablefish thus utilize the neustonic and pelagic environment to rapidly reach sizes at which migration to the benthic adult habitat occurs.

Acknowledgments

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GEORGE W. BOEHLERT

College of Oceanography and Marine Science Center
Oregon State University
Newport, OR 97365
Present address:
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
P.O. Box 3830
Honolulu, HI 96812

MARY M. YOKLAVICH

College of Oceanography and Marine Science Center
Oregon State University
Newport, OR 97365

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